
# Neural Synchronization Patterns During Interpersonal Action Coordination

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## List of original studies

This dissertation is based on the following four papers:

Study I

**Szymanski**, **C**., Pesquita, A., Brennan, A. A., Perdikis, D., Enns, J. T., Brick, T. R., Müller, V., & Lindenberger, U. (2017). Teams on the same wavelength perform better: Inter-brain phase synchronization constitutes a neural substrate for social facilitation. *NeuroImage*, *152*, 425-436.

Study II

**Szymanski, C.**, Brick, T. R., Perdikis, D., Müller, V., Karch, J., & Lindenberger, U. Neural Synchronization during Reciprocal and Parallel Interpersonal Action Coordination. (under review entitled 'Neural Synchronization during Reciprocal and Parallel Dyadic Gaming' at *Frontiers in human neuroscience*).

Study III

Kleinert, M.-L., **Szymanski**, **C**., & Müller, V. (2017). Frequency-unspecific effects of θ-tACS on a visuo-spatial working memory task. *Frontiers in human neuroscience. 11.* 367.

Study IV

**Szymanski**, C., Müller, V., Brick, T. R., von Oertzen, T., & Lindenberger, U. (2017). Hyper-Transcranial Alternating Current Stimulation: Experimental manipulation of inter-brain synchrony. *Frontiers in human neuroscience. 11.* 539.

## Abstract

Social encounters constitute a significant part of human life. They have received increasing attention over the past decade with the rise of two-person or second-person neuroscience. The broader availability of techniques such as hyperscanning, the simultaneous recording of multiple persons' brain activity, has further motivated neuroscientists to study the neural and behavioral dynamics of social interaction and interpersonal action coordination in real-time. The literature on hyperscanning gives ample evidence that inter-brain synchronized patterns emerge during interpersonal action coordination. However, it remains under debate to what extent synchronized patterns between brains reflect specific aspects of social interaction, and serve a mechanistic function. In particular synchronized motor output is often seen as a confounding factor that few studies explicitly control for. In this dissertation, I try to disentangle the contribution of cognitive mechanisms on inter-brain synchronized patterns with a series of empirical studies. Study I investigates the influence of modified attention on inter-brain phase synchronization during an enumeration visual search paradigm. The results suggest that joint attention induces changes in inter-brain phase synchronization that are paralleled by performance increases during teamwork as opposed to individual work. Study II uses a novel paradigm of interpersonal action coordination. It compares reciprocal real-time coordination to parallel coordination with a common driver, while keeping behavioral dynamics comparable across conditions. The results suggest that attentive, predictive, and reactive qualities of interpersonally coordinated actions are associated with inter-brain synchronization, while real-time interaction is not. Study III builds methodological expertise in transcranial alternating current stimulation (tACS) as a means to probe the operation of oscillatory cognitive mechanisms. In Study IV, the tACS setup is extended to the simultaneous phase-locked stimulation of multiple individuals (hyper-tACS). This directly tests a potential relation between inter-brain synchronization and interpersonal synchronization performance during dyadic drumming by attempting to experimentally tune two participants' brains more or less ‚on the same wavelength' using the tACS device. The results of this study suggest that interpersonal drumming synchronicity, but not metronome drumming synchronicity, is influenced by hyper-tACS. Contrary to expectations, both same-phase-same-frequency as well as different-phase-different-frequency stimulations were associated with lower synchronization performance relative to sham control stimulation. In discussing the results of this series of empirical studies, I suggest that the lack of a clear definition of social interaction may be at the origin of controversies about the functional role of inter-brain synchronization patterns. Building on a conceptual framework of interpersonal action coordination, I propose a working definition of social interaction and its cognitive core processes. I suggest to stop trying to disentangle inherent aspects of social interaction, such as synchronized actions, from ‚true social interaction' and instead to focus on the relative influence of attentive, predictive and, reactive mechanisms on inter-brain synchronization and associated behavioral dynamics. I conclude that inter-brain synchronized patterns reflect commonalities in multiple individuals' forward models, regardless whether these commonalities are caused by joint action or not. Asking the question about the functional role of inter-brain synchronized patterns and their

relations to social interaction and interpersonal action coordination from this new perspective may move the hyperscanning field in a more fruitful direction.

## Zusammenfassung

*„Ungeheuer ist viel. Doch nichts Ungeheuerer als der Mensch.“* (Sophokles, *Antigone, Zweiter Akt, Chor der thebanischen Alten.)* Was den Menschen so ungeheuerlich macht, ist unter anderem seine komplexe Interaktion mit anderen Menschen. Seit der Einführung des Konzepts der *two-person* oder *second-person neuroscience* und der *Hyperscanning*-Methodik, das heisst, der gleichzeitigen Messung der Hirnströme mehrerer Individuen zu Beginn des 21. Jahrhunderts, ist das Interesse an sozialer Interaktion in den Neurowissenschaften stetig gewachsen. In der Hyperscanning-Literatur finden sich wiederholt Befunde, die darauf hinweisen, dass synchronisierte Muster zwischen Gehirnen (*inter-brain-Synchronisation*) interpersonale Handlungskoordination charakterisieren und vielleicht konstituieren. Die funktionale Bedeutung dieser Muster wird in der Literatur kontrovers diskutiert, vor allem mit Hinblick darauf, ob diese Muster spezifische Aspekte sozialer Interaktionen oder interpersonale motorische Synchronisation widerspiegeln, unabhängig davon ob diese motorische Synchronisation in soziale Interaktion eingebettet ist oder nicht. Mit einer Serie empirischer Studien untersucht diese Dissertation den Einfluss einzelner kognitiver Mechanismen auf die inter-brain-Synchronisation. Studie I untersucht den Zusammenhang zwischen Aufmerksamkeit und inter-brain-Synchronisation im Kontext einer visuellen Suchaufgabe. Die Resultate dieser Studie legen den Schluss nahe, dass inter-brain-Synchronisation mit modulierter Aufmerksamkeit und besseren Teamleistungen verknüpft ist. Studie II vergleicht, mittels eines neu entwickelten experimentellen Paradigmas, bei konstanter Dynamik der motorischen Handlungen zweier Probanden reziproke und parallele interpersonale Handlungskoordination. Die Ergebnisse dieser Studie legen nahe, dass inter-brain-Synchronisation vor allem motorische Aspekte der Interaktion widerspiegelt. Studie III dient der Erprobung der schwachen Wechselstromtechnologie in unserem Labor (transient alternating current stimulation, tACS). In Studie IV wird diese Technik als *Hyper-tACS* auf zwei miteinander trommelnde Probanden angewandt. Dies soll die direkte Überprüfung eines kausalen Zusammenhangs zwischen inter-brain-Synchronisation und interpersonaler Verhaltenssynchronisation ermöglichen, indem zwei Probanden durch experimentelle Manipulation mittels hyper-tACS auf ‚die gleiche Wellenlänge‘ gebracht werden. Die Resultate dieser letzten Studie zeigen einen komplexen Zusammenhang zwischen inter-brain-Synchronisation und interpersonaler Handlungskoordination, da nur die Synchronisation mit einer anderen Person, nicht jedoch die mit einem Metronom durch hyper-tACS beeinflusst wird. Erwartungswidrig zeigen sowohl die Gleiche-Phase-Gleiche-Frequenz- als auch die Verschiedene-Phase-Verschiedene-Frequenz-Bedingung einen negativen Zusammehang mit der dyadischen Synchronization. In der übergreifenden Diskussion der Befunde meiner Studien zeige ich eine mögliche Ursache für die bisherige Unklarheit der funktionalen Rolle von inter-brain-Synchronisation auf: der Mangel einer Definition sozialer Interaktion in der Hyperscanning-Literatur. Basierend auf Theorien der interpersonalen Handlungskoordination führe ich eine Arbeitsdefinition sozialer Interaktion und der ihr zugrunde liegenden kognitiven Prozesse ein. Die Hyperscanning-Forschung könnte nach meiner Auffassung größere Fortschritte erzielen, wenn sie ihre Aufmerksamkeit vermehrt auf Mechanismen der Aufmerksamkeit, der Handlungsvorhersage und der

Handlungsreaktion richten würde und darauf verzichten würde, inhärente Aspekte sozialer Interaktion, wie synchronisierte Handlungsabläufe, als Störfaktoren zu kontrollieren. Ich schließe diese Dissertation mit der Überlegung, dass inter-brain-Synchronisation Übereinstimmungen der Handlungen und der mentalen Handlungsmodelle mehrerer Individuen reflektiert, und zwar unabhängig davon, ob diese Übereinstimmungen von gemeinsamem Handeln begleitet werden oder nicht.

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## List of abbreviations

**ANOVA..... analysis of variance**
**b..... beta**
**EEG..... electroencephalography**
**ICA..... independent component analysis**
**IPC..... inter-brain phase coherence**
**Hz..... Hertz**
**fMRI..... functional magnetic resonance imaging**
**fNIRI..... functional near-infrared imaging**
**mc-PLS..... mean-centered partial least squares analysis**
**mTs..... match-to-sample task**
**NIRS..... near-infrared spectroscopy**
**nr-PLS..... non-rotated partial least squares analysis**
***p*..... p-value**
**PLI..... phase locking index**
**PLS..... partial least squares analysis**
**R2..... R-adjusted**
**SD..... standard deviation**
**SE..... standard error**
**singular value..... s**
**tACS..... transcranial alternating current stimulation**
**tDCS..... transcranial direct current stimulation**

# 1 Introduction

„The best portion of your life will be the small, nameless moments you spend smiling with someone who matters to you.“ - Ritu Ghatourey

Human life is social interaction and shared moments with others are among the most important things for all of us. With this dissertation, I provide a new way of thinking about the role of synchronized neural patterns in social interaction. Metaphorically speaking, I take a neuroscientific look at the expression ‚being on the same wavelength with someone‘. Scientifically speaking, I investigate the role of inter-brain synchronized patterns during social interaction and interpersonal action coordination. Mental representations of action goals and actions have been suggested to underlie individual and interpersonally coordinated actions (Sänger, Lindenberger, & Müller, 2011; Wolpert and Ghahramani, 2000) and inter-brain synchronized patterns have been suggested to reflect these represenations of both one’s own and one’s partner’s actions during coordinated action (Sänger et al., 2011). As an alternative to this representational account, direct perception-action links relying on a dynamical systems framework have been suggested, especially in the context of simple actions that do not involve planning, but instead require precise temporal coordination, short-term predictions and adaptations to others’ behavior (Marsh, Johnston, Richardson, & Schmidt, 2009; Schmidt & Richardson, 2008). This second approach to interpersonal action coordination has yet been applied relatively little to the study of inter-brain synchronized patterns.

In the following section, I will give an overview about the nature of inter-brain synchronized patterns, the techniques used to study them, and the current state of the literature on inter-brain synchronized patterns with a focus on their hypothesized relation to interpersonal action coordination.

## 1.1 Empirical overview of inter-brain synchronized patterns

*Inter-brain synchronized patterns* delineate patterns of relative timing in the neural activity of two or more people. The type of observed patterns depends on the chosen recording and analysis techniques. While inter-brain synchronized patterns are generally investigated using the *hyperscanning technique*, the simultaneous recording of multiple subjects’ brain activity, the form of recording varies: so far, fMRI (Montague et al., 2002), EEG (Babiloni et al., 2007), NIRS (Cui, Bryant, & Reiss, 2012) and MEG (Baess et al., 2012) have been used as recording techniques.

With its high spatial resolution (typically in the millimeter range or even lower; Goense, Bohraus, & Logothetis, 2016) fMRI is best suited to offer a high resolution, simultaneous view of the functional neuroanatomy of two or more human brains engaged in a social interaction. The use of fMRI hyperscanning for the study of social interaction and interpersonal action coordination is however limited by two factors. First by the rigid setup the fMRI technique, which requires participants to lay still in the scanner and moreover it is difficult to connect two or more scanners to truly hyperscan subjects simultaneously, so instead they are often scanned one

after another (although there have been proof-of-concept studies; Lee, 2009; Montague et al., 2002; Trees et al., 2014). Second, the low temporal resolution of fMRI (Kim, Richter, & Ugurbil, 1997) limits a more detailed investigation of temporal synchronization patterns. Yet, precisely the question “how individuals adjust their actions to those of another person in time and space“ (Sebanz, Bekkering, & Knoblich, 2006, p. 73) has been put forward as one core question in the study of interpersonal action coordination.

Thanks to its high temporal resolution in the range of milliseconds EEG hyperscanning is ideally suited to study temporally synchronized inter-brain patterns, although its spatial resolution is limited and in particular complicated by the inverse-problem for source reconstruction (Grech et al., 2008). EEG hyperscanning is much more flexible in its setup than fMRI. Thus, it is possible to measure participants' brain activity truly simultaneously and to further study interpersonal coordination in ecologically valid settings. Of note, EEG hyperscanning has already been pioneered in 1965 when Duane and Behrend used it to study potential thought transmission (Duane, 1965). The third variant of hyperscanning is also applicable in ecological setups and uses near-infrared spectroscopy (NIRS) or functional near-infrared imaging (fNIRI). Recently, even a wearable multi-channel fNIRI system has been introduced (Piper et al., 2014). NIRS measures changes in oxyhemoglobin and deoxygenated hemoglobin with medium temporal and spatial resolution (~10 Hz, 1-3cm; see Cui, Bray, Bryant, Glover, & Reiss, 2011; Strait & Scheutz, 2014). Similar to EEG, an inherent limitation of the NIRS technology is its limitation to measure cortical brain regions only, and not sub-cortical areas (Scholkmann, Holper, Wolf, & Wolf, 2013). MEG hyperscanning has been pioneered recently (Baess et al., 2012) and is a promising tool to complement investigation of time-frequency synchronized patterns using EEG with high spatial resolution. This might be particularly interesting with regard to the relation of ‚classical‘ neuroanatomical networks such as the theory-of-mind network (Fletcher et al., 1995) to synchronized neural patterns across brains. In the following, I will give an overview of the current state of the literature on hyperscanning using the three major technologies, fMRI, EEG and NIRS.

### 1.1.1 FMRI hyperscanning

The term *hyperscanning* was introduced to what is now referred to as ‚two-person neurosience‘ (Hari & Kujala, 2009) using fMRI in a pioneering study by Montague (Montague et al., 2002). Subsequently, several authors turned to fMRI hyperscanning to study inter-brain synchronized patterns during communication and cooperation. Hasson and colleagues used spatiotemporal neural patterns recorded from one participant while watching a movie sequence to predict the spatiotemporal patterns of several other subjects watching the same movie sequence. Not only visual and auditory, but also association cortices showed synchronized activity patterns (Hasson, Nir, Levy, Fuhrmann, & Malach, 2004). This finding was further extended to synchronized neural patterns across participants when viewing similar emotional events in a movie (Nummenmaa et al., 2012). Stephens and colleagues analogously used fMRI hyperscanning to assess speaker-listener synchronized patterns and regional differences in timing and strength of speaker-listener coupling

and reported a correlation between speaker-listener synchronized neural patterns and listener's story comprehension (Stephens, Silbert, & Hasson, 2010). King-Casas and colleagues (2005) studied inter-brain patterns in an economic trust game. They reported a correlation between activity in the trustee's anterior cingulate cortex with activity in the investor's middle cingulate cortex 14 seconds earlier. Schippers and colleagues (Schippers, Roebroeck, Renken, Nanetti, & Keysers, 2010) reported that activity in the sender's brain proceeded activity in the perceiver's brain during charade gesturing. Anders and colleagues (Anders, Heinzle, Weiskopf, Ethofer, & Haynes, 2011) corroborated this result for facial communication. The authors were able to predict the perceiver's brain activity from the sender's preceding brain activity. Similarly, during an information exchange paradigm Bilek and colleagues (2015) detected a dependency between activity in the sender's and the receiver's temporoparietal junction, which further correlated with mean real-life social network complexity. Saito and colleagues (2010) studied joint attention during real-time gaze exchange. Interpersonal correlation analysis of time-series activity revealed higher correlations in the right inferior frontal gyrus, in pairs that interacted as compared to pseudo-pairs. Similarily, Koike and colleagues (2016) investigated synchronized patterns during a mutual-gaze paradigm and report a correlation between enhanced eye-blink synchronization and inter-individual neural synchronization within the right inferior frontal gyrus. Taken together, studies using fMRI hyperscanning have consistently reported inter-brain synchronized patterns during communication and cooperation, localized mostly in pre-frontal and frontal cortical structures. Asymmetric temporal relationships between neural activity were repeatedly associated with different sociocognitive roles.

### 1.1.2 EEG hyperscanning

Due to its restrictive setting that requires participants to lay still in the scanner, fMRI hyperscanning is not well-suited for the study of joint action. Thus many researchers have turned to EEG hyperscanning as it offers high temporal resolution and relatively easy handling that makes it possible to record participants' brain activity truly simultaneously and to study interpersonal coordination in ecologically valid settings, such as card game play (Babiloni et al., 2007), guitar play (Lindenberger, Li, Gruber, & Müller, 2009; Sänger, Müller, & Lindenberger, 2013), flight simulation (Astolfi et al., 2011), romantic kissing (Müller & Lindenberger, 2014) or real-life classroom teaching (Dikker et al., 2017). These studies, as well as studies using simpler paradigms such as imitation (Dumas, Nadel, Soussignan, Martinerie, & Garnero, 2010; E. Tognoli, J. Lagarde, G. C. DeGuzman, & J. A. Kelso, 2007a), repeadtely reported synchronized brain activity between two or more people engaged in the same task (Lindenberger et al., 2009; Nadel, 2014; Sänger, Müller, & Lindenberger, 2012; Tognoli et al., 2007a; Yun, Watanabe, & Shimojo, 2012). Inter-brain synchronized patterns are generally analyzed with respect to EEG power (Konvalinka et al., 2014), the engagement of particular brain regions (Babiloni et al., 2006) and frequencies (Müller & Lindenberger, 2014; Tognoli et al., 2007a). As with fMRI hyperscanning, synchronized patterns were reported for speaker-listener interaction, peaking at a time delay of 12.5s, which the authors interpreted as evidence that listeners coordinate with speakers at the level of complex semantic representations (Kuhlen, Allefeld, & Haynes, 2012). Asymmetrical patterns between

two brains have for example been reported during dyadic fingertapping (Konvalinka et al., 2014), guitar duet play (Müller, Sänger, & Lindenberger, 2013), imitation (Dumas et al., 2010; Tognoli et al., 2007a) or card game play (Babiloni et al., 2007). These asymmetrical patterns have again been associated with different sociocognitive roles, in particular those of leader and follower. Applying Granger causality and graph theory to EEG hyperscanning data during card game play, Astolfi and colleagues showed that the strategic leader's activity at prefrontal sites was associated with their partner's activity in the anterior cingulate cortex (Astolfi et al., 2010). Similarly to the fMRI studies by Saito and colleagues (2010) and Bilek and colleagues (2015), this interdependence was not observed for players that belonged to different teams. Another focus of several studies were changes in inter-brain synchronized patterns between cooperative and competitive scenarios. De Vico Fallani and colleagues (De Vico Fallani et al., 2010) reported a dependency between the strength of inter-brain synchronized patterns, mostly in pre-frontal regions in the beta and gamma frequency band, and partner cooperation in the prisoner's dilemma paradigm. Mu, Guo and Han (2016) experimentally administered Oxytocin in male participants and reported subsequent increases in differences in inter-brain synchronization between cooperation and a control task, which were particularly prominent in the alpha frequency band. Moreover, increased inter-brain synchronization correlated with increased behavioral dyadic synchronization. Kawasaki, Yamada, Ushiku, Miyauchi and Yamaguchi (2013) reported a similar observation using a speech synchronization paradigm. Inter-brain synchronization in temporal and parietal regions at 6-12Hz was enhanced during human-human interaction as opposed to human-machine interaction. This increase in inter-brain synchronization was paralleled by an increase in speech rhythm synchronization between participants. Dikker and colleagues (2017) reported higher inter-brain synchronization in a group of students that corresponded to higher classroom engagement. The focus on time-frequency patterns and "phase-coupled neural signals across multiple brains" (Novembre, Knoblich, Dunne, & Keller, 2017, p. 662) has received much attention in the EEG hyperscanning literature.

Different measures have been suggested to study these neural patterns (Burgess, 2013; Lindenberger et al., 2009) inter-brain phase coherence (IPC), also sometimes referred to as phase-locking value, being amongst the most popular measures. Tognoli and colleagues (E. Tognoli, J. Lagarde, G. C. DeGuzman, & J. A. S. Kelso, 2007b) suggested in particular oscillations in the alpha frequency range at right centro-parietal sites as a ‚neuromarker of human social coordination'. Synchronized patterns in centro-parietal electrode connections have also been reported in several other studies. (Astolfi et al., 2011; Lindenberger et al., 2009; Müller & Lindenberger, 2014; Sänger et al., 2012; Tognoli et al., 2007a). However, although reported for similar regions, the peak frequency of the reported synchronized patterns differed between studies. While the results of some studies support the view by Tognoli and colleagues that the alpha band plays a particularly prominent role for inter-brain synchronization during interpersonal action coordination (Dumas et al., 2010; Konvalinka et al., 2014), others have also reported pronounced inter-brain synchronization at different frequency bands, such as delta and theta (Müller & Lindenberger, 2014; Müller et al., 2013; Sänger et al., 2012) or also beta and gamma (De Vico Fallani et al., 2010; Dumas et al., 2010). Across EEG hyperscanning studies, inter-brain synchronization was consistently reported for

interpersonal action coordination. It was generally rather observed for various electrode-connections and frequencies than strictly confined to one region and frequency band. Correlations with behavioral performance were reported in a number of studies using diverse paradigms.

### 1.1.3 NIRS hyperscanning

The temporal resolution of NIRS is inferior to the temporal resolution of EEG. Thus, the findings on inter-brain synchronized patterns in the beta and gamma band (see e.g. De Vico Fallani et al., 2010; Dumas et al., 2010; Menoret et al., 2014) likely constitute one reason why NIRS hyperscanning is less popular than EEG hyperscanning. However, its relatively lower cost and easier handling make NIRS nevertheless an attractive technology that is repeatedly used in hyperscanning studies. Results are generally in line with those obtained using fMRI or EEG hyperscanning. For example several studies reported increased inter-brain synchronization in particular at frontal and pre-frontal sites for cooperation as compared to competition/parallel play (Cui et al., 2012; Duan et al., 2013; Funane et al., 2011; N. Liu et al., 2016) in paradigms involving more simple (e.g. button press, Cui et al., 2012; Funane et al., 2011) and more complex movements, (e.g. Jenga-game play, N. Liu et al., 2016). Pan, Cheng, Zhang, Li, and Hu (2017) investigated the impact of emotional affection on inter-brain synchronized patterns. They had stranger-dyads, friend-dyads and lover-dyads perform a task analogue to the one used by Cui and colleagues (2012). They reported strongest inter-brain synchronization for pairs of lovers, that was paralleled by strongest behavioral synchrony between lovers. Ikeda and colleagues (2017) had groups of 35 subjects walk in synchrony. Group walking synchronicity increased when subjects were instructed to adjust their paces to a steady beat and translated to increases in inter-brain synchronization at < 0.1Hz. However, inter-brain synchronization did not increase in a control condition of group stepping to beat. The authors interpret the difference between group stepping and group walking in that only the latter necessitates interpersonal action coordination and thus it is precisely social interaction that impacts neural synchronized patterns here. Jiang and colleagues (Jiang et al., 2012) investigated the relation between the behavioral dynamics of interpersonal interaction and inter-brain synchronization. The authors reported increased inter-brain synchronization during face-to-face dialogue compared to back-to-back dialogue. They interpreted their results in that particularly behavioral dynamics (turn-taking and body language, e.g. facial expressions and gestures) contribute to increases in inter-brain synchronization. Jiang and colleagues (2015) reported stronger inter-brain synchronization for leader-initiated communication than for follower-imitated communication but did not investigate if these relative changes in inter-brain synchronization were paralleled by differences in behavioral dynamics of leader-initiated and follower-initiated communication. Interestingly, also physical similarities have been shown to impact inter-brain synchronization. Cheng, Li and Hu (2015) reported differences in inter-brain synchronized patterns for same-sex pairs as opposed to different-sex pairs during a cooperation task. Using computational modeling Dumas and colleagues suggest that anatomical connectivity may influence inter-brain synchronization (Dumas, Chavez, Nadel, & Martinerie, 2012).

To summarize, studies using the different hyperscanning methods have repeatedly reported associations between inter-brain synchronized patterns and behavioral synchronization (see e.g. Dumas et al., 2010; Ikeda et al., 2017; Jiang et al., 2012; Konvalinka et al., 2014; Lindenberger et al., 2009; Mu et al., 2016; Pan et al., 2017). Further, asymmetries in inter-brain synchronization have repeatedly been associated with different sociocognitve roles, such as leader and follower (Jiang et al., 2015; Konvalinka et al., 2014) or sender and receiver (Dumas et al., 2010). These inter-brain asymmetries have again been linked to asymmetries in the behavioral dynamics that result from differing sociocogntive roles (Jiang et al., 2012). While the phenomenon of inter-brain synchronized patterns during interpersonal action coordination has been established in the literature, no consensus on their functional meaning for interpersonal action coordination and social interaction has yet been reached (Hari, Henriksson, Malinen, & Parkkonen, 2015; Konvalinka & Roepstorff, 2012; T. Liu & Pelowski, 2014b) This is precisely the ‚white spot on the literature map', which this dissertation aims to address.

### 1.2 Social interaction, synchronized behavior, and inter-brain synchronized patterns

The rising popularity of inter-brain synchronization (Konvalinka & Roepstorff, 2012) has partly been caused by and partly resulted in the rising popularity of ‚two-person neuroscience' (Hari & Kujala, 2009) or ‚second-person neuroscience' (Schilbach et al., 2013). As Hari and colleagues (2015) put it: "Instead of emerging from lower-level cognitive functions, social interaction could be the default mode via which humans communicate with their environment." (Hari et al., 2015, p. 1). The idea that interaction is central to social cognition mainly dates back to the seminal book ‚The Embodied Mind' (1991) by Varela, Thompson and Rosch. Central to *embodiment* is the idea that biological brains have not developed to control how a biological system represents and interacts with the outer world, but precisely because a biological system interacts with its surrounding outer world. The sea squirt is put forward as interesting evidence for this claim: The moving larva has well-developed brains. Once it metamorphoses into adulthood, it stops moving and settles on the sea ground and its neural structures are reduced (Cameron, Garey, & Swalla, 2000). *Embodiment* thus suggests that in order to understand the mechanisms of (social) cognition, one needs to study individuals engaged in interaction. Recently, these ideas have been reformulated for example as the ‚second-person approach to other minds' (Schilbach et al., 2010). Here the main focus is on the active, interactor's perspective which is contrasted with the passive, spectator's perspective (Gallotti & Frith, 2013; Schilbach et al., 2013). Eventually, the question ‚how can mutually interacting brains teach us something about social interaction?' (Konvalinka & Roepstorff, 2012) moves the idea of embodiment and second-person perspective into the realm of hyperscanning and inter-brain synchronized neural patterns. But while many authors stress the importance of interaction for social cognition, no popular definition of social interaction is put forward in the hyperscanning literature. Thus, it often remains illusive what cognitive and neural mechanisms are precisely hypothesized to differ when two individuals are in interaction as opposed to when they are acting individually (Gallotti & Frith, 2013; Konvalinka & Roepstorff, 2012). Several authors have criticized the hyperscanning literature for a lack of careful

control conditions that isolate the impact of social interaction from confounding factors (Burgess, 2013; Hari et al., 2015; Konvalinka & Roepstorff, 2012; T. Liu & Pelowski, 2014b). Anatomical structures (Dumas et al., 2012), differences in experimental conditions (Burgess, 2013), and synchronous physiological changes during interpersonal coordination, such as cardiac or respiratory signals (Müller & Lindenberger, 2011) could all manifest as spurious correlations in inter-brain synchronized patterns. In particular synchronized motor actions (Hari et al., 2015; Lindenberger et al., 2009; T. Liu & Pelowski, 2014b) have been highlighted as one potential cause for inter-brain synchronization, ‚having little to do with the presence of the other human.' (T. Liu & Pelowski, 2014b, p. 1).

## 2 Research questions and hypotheses

In the previous sections, I outlined that: (A) interpersonal coordination has been repeatedly associated with inter-brain synchronized patterns; (B) the functional role of these inter-brain synchronized patterns remains under debate, particularly with respect to the function of inter-brain synchronization for social interaction and interpersonal action coordination. The aim of this dissertation is to advance our understanding of the functional role of inter-brain synchronized patterns for social interaction and interpersonal action coordination. Specifically, this dissertation investigates (A) if inter-brain synchronization is modulated by joint attention, and (B) if real-time reciprocal interaction and the similarity of behavioral dynamics modulate inter-brain phase synchronization. Finally, this dissertation investigates (C) if inter-brain phase synchronization provides a mechanism for the temporal alignment of actions between individuals.

This thesis is thus structured around two major research questions.

(1) Does inter-brain phase synchronization reflect characteristics of interpersonal action coordination other than perceptual input/motor output similarity?

(2) How is inter-brain phase synchronization related to interpersonal action coordination performance?

Study I addresses these two overarching questions by focusing on a core aspect of interpersonal action coordination, namely joint attention. The specific research questions for study I are the following:

(A) Is inter-brain phase synchronization sensitive to the presence of ‚the other', thus does inter-brain phase synchronization differ between individual and joint attention under identical perceptual input?

(B) Do between-pair differences in inter-brain phase synchronization during joint attention correlate with between-pair differences in behavioral performance on a teamwork task?

Study II addresses the two major research questions by comparing inter-brain phase synchronization across reciprocal interpersonal action coordination, parallel interpersonal action coordination preserving the same behavioral dynamics, and intra-personal action coordination with different behavioral dynamics. It addresses the following specific research questions:

(A) Does inter-brain phase synchronization differentiate between reciprocal and parallel coordination following the same behavioral dynamics, thus, is it sensitive to the presence of interaction as such?

(B) Does inter-brain phase synchronization differentiate between conditions that differ in their behavioral dynamics, thus is it sensitive to differences in motor output similarity?

Study III is a preparatory study for Study IV. By attempting to replicate results reported by Polania and colleagues (2012) using a working memory paradigm adopted from Griesmayr and colleagues (2014) the study aimed to establish the tACS methodology in our lab before extending it to the application of hyper-tACS in Study IV. As a pre-study to Study IV, Study III used a stimulation protocol that we adopted to two-person stimulation in Study IV. The specific research hypotheses and results of Study III will not be elaborated, as study III is used specifically to establish a methodological base on which to build with Study IV.

Study IV tests the second major research question directly through experimental manipulation of inter-brain phase synchronization. Effects on dyadic drumming synchronization performance are investigated. Study IV specifically tests the following research questions:

(A) Does same-phase-same-frequency hyper-tACS improve dyadic drumming synchronization, while different-phase-different-frequency hyper-tACS deteriorates dyadic drumming synchronization?

(B) Do metronome drumming synchronization as well as individual and dyadic preferred drumming tempo remain unaffected by hyper-tACS?

# 3 Methods

I investigate the role of inter-brain phase synchronization in social interaction and interpersonal action coordination with four empirical studies. To measure inter-brain phase synchronization during interpersonal coordination I used EEG hyperscanning in Study I and Study II. Study III served to setup the tACS methodology in our lab as a preparation for Study IV, where I used hyper-tACS to experimentally manipulate inter-brain synchronization during interpersonal action coordination. In the following section I will layout the experimental setups and paradigms used in these empirical studies.

## 3.1 EEG hyperscanning setup

Participants were comfortably seated back-to-back in an acoustically and electromagnetically shielded EEG cabin. Each participant faced a computer screen placed on a table directly in front of them. Displays subtended 37° x 30° visual angle on a 19-inch computer monitor (screen resolution 1280 x 1024 pixels). EEG measurement took place continuously throughout the experimental session. The EEG was recorded with active 64 Ag/AgCl electrodes per person, placed according to the international 10–10 system, with the reference electrode at the right mastoid

(actiCAP, Brain Products, Munich, Germany). Separate amplifiers (BrainAmp DC, BrainProducts, Munich, Germany) with separate grounds were used for each individual, linked to one computer. Vertical and horizontal electrooculograms were recorded to control for eye blinks and eye movements. All channels were recorded at a sampling rate of 5000 Hz. A 0.016–1000 Hz bandpass filter was used. Triggers

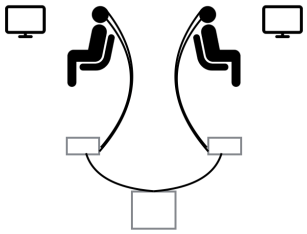


Figure 1. Experimental EEG hyperscanning setup. Simultaneous EEG measurement of two participants. Both participants are connected to an amplifier each. Amplifiers are connected to the same computer.

were sent from the stimulus presentation computer to the EEG-recording system for stimulus onset. One stimulus computer was connected to three synchronized screens for stimulus presentation. Two screens were placed inside the cabin whereas one control display was placed outside the EEG cabin to monitor stimulus presentation. Data were resampled at 1000 Hz after the recordings and subjected to semi-automatic independent component analysis (Vigário, 1997) as implemented in Brain Vision Analyzer 2 as Ocular Correction independent component analysis (Brain Products). Using visual inspection of topographies and time courses, components that reflected blinks, horizontal eye movements, electrocardiogram, muscle activity and line noise were removed during data preprocessing.

### 3.2 Hyper-tACS setup

Electrical stimulation was delivered through a four-channel direct current stimulator (DC-Stimulator MC; NeuroConn GmbH, Ilmenau, Germany). The tACS stimulator was connected to three conductive rubber electrodes (each 5x5 cm). We placed two stimulation electrodes each subject's right hemisphere F4 (fronto-central) and P4 (parieto-central) of the international 10-20 system. As a multichannel stimulator system was used, each stimulation electrode was connected to one independent channel and both cables of these corresponding return channels were electromechanically soldered into one single merged cable for the return electrode, which was placed on Cz (central). Impedance was kept below 20kOhm throughout the stimulation session. Stimulation intensity was ramped up to the maximum intensity of 1mA over 30s and ramped off to zero for 30s after the stimulation. Stimulation was automatically ended after 25min. Three different stimulation parameters were used for each dyad in a pseudo-randomized cross-over design. All stimulations were alternating current sinusoidal stimulation: (a) 'same-phase-same-frequency stimulation': both subjects received stimulation at 6Hz with a zero phase difference; (b) 'different-phase-different-frequency stimulation': one subject received 5Hz with 13 degrees offset, the other 7Hz with 1 degree offset; (c) 'sham stimulation': both subjects received 30s fade-in and 30s fade-out 6Hz stimulation.

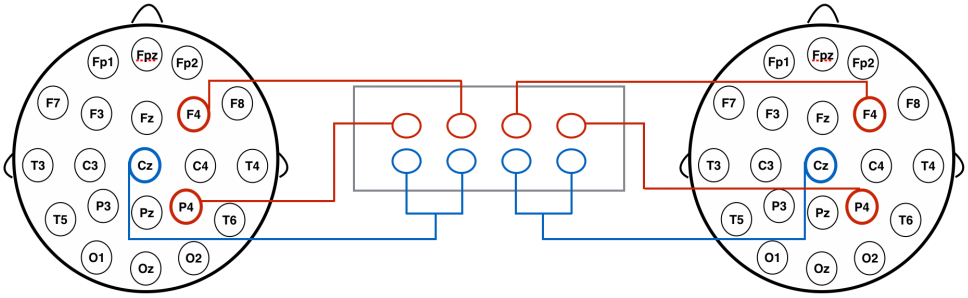



Figure 2. Experimental hyper-tACS setup.
Electrode placement and cable connections to four-channel direct current stimulator are shown. red = stimulation electrodes. blue = return electrodes.

### 3.3 Enumeration visual search paradigm (Study I)

Experimental displays depicted shelves containing objects commonly found in a home or office (see Figure 3 for an example display). Each display contained 82 distractor objects in one of four different configurations, and zero, one, or two of four possible target objects. The same target never appeared twice in the same display and each appeared equally often in each quadrant. This generated 356 displays: four without a target, 64 with one target, and 288 with two targets. Experimental sessions consisted of a total of 42 trials: 14 trials each with zero, one, and two targets. Search displays for each session were selected using weighted random sampling of the 356 total search displays. Displays subtended 37° x 30° visual angle on a 19-inch computer monitor (screen resolution 1280 x 1024 pixels). Matlab 2010a software and Psychtoolbox3 were used to control the experiment. During the experiment participants indicated as rapidly and accurately as possible the number of targets present in a display by pressing keys labeled ‘0’, ‘1’, and ‘2’. Participants completed two experimental sessions: one individually (individual condition) and one as a team with another participant (social condition). Session order was randomly counterbalanced across pairs (individual first, social first). When completing the task individually, participants sat in front of their respective computers and entered responses on their respective keyboard. When completing the task as a team, participants sat side by side in front of a shared computer and entered one joint response using a shared keyboard. One participant replied during the first half of the experiment, the other participant during the second half. Teams were instructed to use whatever strategy they thought was best for working together and individuals were instructed to use whatever strategy they thought was best. Participants received feedback about their percentage of correct responses every seven trials.

### 3.4 Interactive virtual paradigm ‚stay with me‘ (Study II)

The novel interactive virtual game ‘stay with Me’ was specifically designed for this study and implemented in C++. Each 90-second-trial started with two circles (red/blue, with a distance of 400 pixels) displayed at the center of the screen; immediately squares began to fall and rise vertically across the screen (100x100

pixel, speed varies between 2-4 pixel/16ms, at any given point in time there were between 4 and 15 squares present on the screen). The participants' task was to (a) navigate the circles through the squares while (a) avoiding collisions with the squares and while (b) maximizing spatial overlap between their circles (see Figure 9 B for an example display). Each participant controlled direction and speed of one circle (red/blue, diameter 100 pixel, speed = 1-4 pixel/16ms). At the end of each trial, feedback on performance (number of collisions and circle overlap score) was displayed in the upper right corner. Participants then indicated perception of control by button press. ('Who determined the course of the game'? 1= me, 5 = jointly, 9=my partner). One practice trial familiarized participants with joystick handling (40 seconds) before the study began. The study consisted of 21 pseudorandomized trials divided into four conditions (*reciprocal (*described above), *replay*, *replay other*, *alone*). In all four conditions participants interacted with their environment (the squares). *Reciprocal* was a case of reciprocal interpersonal action coordination, where the two participants both navigated one circle each and additionally interacted with each other (each other's circles). *Replay* was a case of parallel interpersonal action coordination. Identical to *reciprocal* in perceptual input, in *replay* both players saw their own and the second circle on their respective screen. However, now this second circle was not their partner's active circle, but a circle that replayed the circle movements that had been recorded on an earlier *reciprocal* trial. Although this replayed circle was not reactive, the coordination dynamics contained in its movement contained the signature of reciprocal coordination. Thus, in trials where I was replaying my opponent, if I respond to the same stimuli the same way, coordination dynamics were identical to the *reciprocal* trial that was being replayed. In *replay*, both participants were always shown an identical recording: in 50% of replay trials both participants coordinated with the circle movements that had been recorded from participant A, in 50% with the circle movements that had been recorded from participant B, to balance 'me-replays' and 'partner-replays'. *Replay other* was also a case of parallel interpersonal action coordination, but different from *replay* in that the recording came from a reciprocal trial from a different pair and coordination dynamics were thus not endemic to the dyad, but different and more difficult to predict. Finally, *alone* was a condition identical to *replay* and *replay other* in that there was no interaction between the participants. Additionally however, behavioral dynamics differed more between the participants. In *alone*, analogue to the other three conditions, each participant was navigating one circle each, but in contrast they did not see a second circle on the screen and their only goal was avoiding collisions with squares.

### 3.5 Dyadic drumming setup (Study IV)

Participant pairs were seated back-to-back in an acoustically and electromagnetically shielded cabin with a portable wall separating both participants. Both participants drummed with the drumsticks in their right hands. Drum beats were digitized (Roland drum computer, Germany) and along with auditory instructions and metronome beats (both sent from Intel Xeon, 3.7GHz PC running Windows 7) played to participants through in-ear headphones, covered by additional soundproof headphones. Drum beat data was recorded from two redundant sources. First, sensors (BIOVISION; single axis, sensitivity: 50 g) attached to the

top end of the drumsticks recorded drumstick acceleration, and a peak detection algorithm was used to determine at which exact time points (in milliseconds) drum beats occurred. Second, the digitized drum beat signals were recorded directly via an ExG bipolar amplifier (Brain Products, Munich, Germany) on a second computer (Intel Core i5, 3.2 GHz running Windows XP).

# 4 Empirical studies

## 4.1 Study I: inter-brain phase synchronization during joint attention

**Szymanski**, **C**., Pesquita, A., Brennan, A. A., Perdikis, D., Enns, J. T., Brick, T. R., Müller, V., & Lindenberger, U. (2017). Teams on the same wavelength perform better: Inter-brain phase synchronization constitutes a neural substrate for social facilitation. *NeuroImage*, *152*, 425-436.

**Background.** Studies using the EEG hyperscanning technology have repeatedly reported synchronized neural patterns between the brains of two interacting individuals (Babiloni et al., 2007; Dumas et al., 2010; Lindenberger et al., 2009; Müller & Lindenberger, 2014; Sänger et al., 2011; Tognoli et al., 2007a). So far, the majority of studies in the field of hyperscanning research have focused on joint action. The settings explored range from highly restricted tasks such as finger tapping (Konvalinka et al., 2014) to ecologically valid tasks such as guitar duet play (Lindenberger et al. 2009, Müller et al. 2013, Sänger et al., 2012, 2013) or conversation (Jiang et al., 2015). A major critique to many of the hyperscanning


Figure 3. Experimental set-up in the electromagnetically shielded cabin.
A. EEG measurement of one participant in the individual condition. B. Two participants being measured in the social condition. C. Example of a search display.

studies mentioned has been the lack of a proper control condition: Namely, a condition devoid of social context, which keeps perceptual input and motor output constant relative to the social condition. Thus, in Study I we introduced an enumeration visual search paradigm that focused on an essential aspect of joint action that involves minimal motor output: joint attention.

**Aims.** We aimed (a) to clarify if increases in inter-brain phase synchronization are associated with social interaction in the absence of synchronized motor output and (b) to investigate if increased phase synchronization during social interaction is associated with behavioral performance gains upon teamwork.

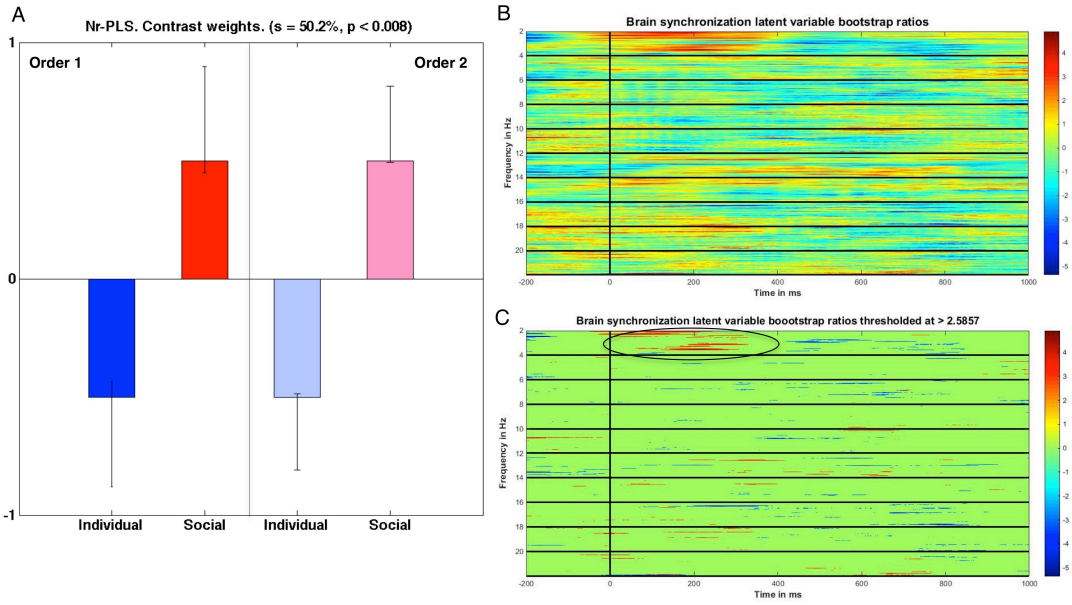



Figure 4. Nr-PLS on PLI revealed higher PLI values in the social condition. A. Mean of subjects' brain scores per condition, mean-centered and normalized with the corresponding singular value (s), and 95% confidence intervals (CI) derived from the bootstrap test. Order 1 = session order with the individual condition first. Order 2 = session order with the social condition first. B. Brain synchronization latent variable bootstrap ratios before thresholding. Each horizontal line corresponds to one electrode at the indicated frequency (42 channels per frequency, grouped from frontal to occipital within frequencies). The colormap is anchored at the lowest and highest values. X-axis: time in ms; Y-axis: channels grouped by frequency (black lines indicate frequency boundaries) C. Analogue to (B) with brain synchronization latent variable bootstrap ratios thresholded at bootstrap ratios > 2.5857 (99% CI). Strongest effects indicated by black ellipses.

**Hypotheses.** Based on previous findings in the EEG hyperscanning literature (see for review: Konvalinka & Roepstorff, 2012; Sänger et al., 2011) we hypothesized that (a) Inter-brain synchronization would be greater in a social context than in a comparable setting that does not engage joint attention; (b) between-pair differences in inter-brain neural dynamics would correlate with between-pair differences in task performance.

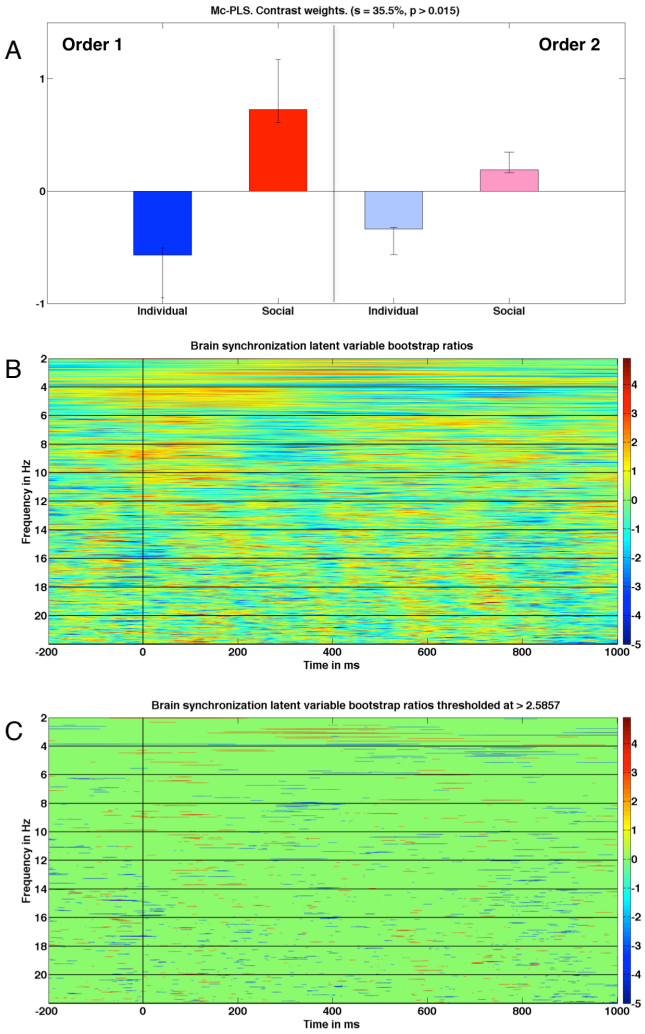



Figure 5. Ms-PLS IPC reveals higher IPC values in the social condition. A. Mean of subjects' brain scores per condition, mean-centered and normalized with the corresponding singular value (s), and 95% confidence intervals derived from the bootstrap test. B. Brain synchronization latent variable bootstrap ratios before thresholding. Each horizontal line corresponds to one electrode connection at the indicated frequency (441 connections per frequency, grouped from frontal to occipital within frequencies). The colormap is anchored at the lowest and highest values. x-axis: time in ms. y-axis: channel connections grouped by frequency (black lines indicate frequency boundaries). Panel C shows brain synchronization latent variable bootstrap ratios after thresholding at bootstrap ratios > 2.5857 (99% CI).

**Methods.** To address our research questions we used an enumeration visual search task previously established by Brennan and Enns (2014) in combination with EEG hyperscanning in same-sex dyads (N = 26, 13 female-female, mean age of participants = 25.2, SD = 3.43; see Figure 3 for experimental setup and example search display). We analyzed behavioral performance analogue to Brennan and Enns (2014) to obtain a measure of team efficiency, which reflected behavioral performance change from searching the displays individually to searching them as a team. We restricted the EEG analysis to the first second of each trial, to capture a period of individual/joint attention free of movement artifacts, such as button press. We calculated phase locking index (PLI) as a measure of local phase synchronization, inter-brain phase coherence (IPC) as a measure of inter-brain phase synchronization and intra-brain phase synchronization as a measure of general intra-brain coherence. We used partial least squares to assess changes in PLI and IPC between individual and joint attention and then inserted ‚brain scores' derived by PLS into a series of hierarchical regression analyses to evaluate how well brain phase synchronization predicted behavioral team performance.

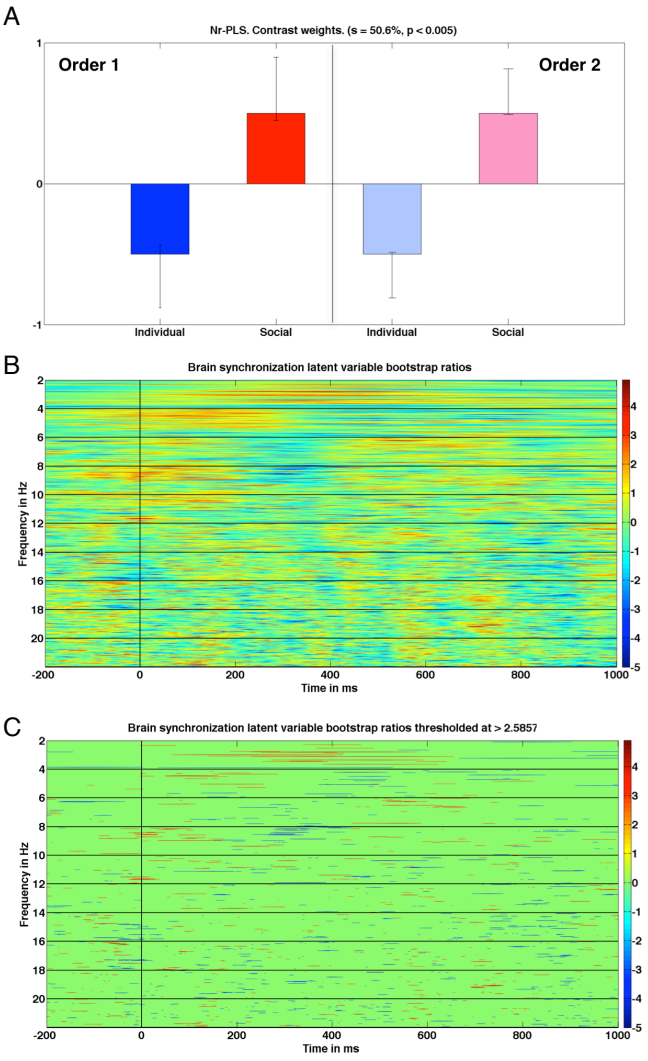



Figure 6. Nr-PLS IPC reveals higher IPC values in the social condition. A. Mean of subjects' brain scores per condition, mean-centered and normalized with the corresponding singular value (s), and 95% confidence intervals derived from the bootstrap test. B. Brain synchronization latent variable bootstrap ratios before thresholding. Each horizontal line corresponds to one electrode connection at the indicated frequency (441 connections per frequency, grouped from frontal to occipital within frequencies). The colormap is anchored at the lowest and highest values. x-axis: time in ms. y-axis: channel connections grouped by frequency (black lines indicate frequency boundaries). Panel C shows brain synchronization latent variable bootstrap ratios after thresholding at bootstrap ratios > 2.5857 (99% CI).

**Results.** The results confirmed our hypotheses. Both, local (Figure 4) and inter-brain phase synchronization (Figures 5 and Figure 6), were increased during joint attention relative to individual attention. A strong increase in PLI during the social condition was especially observed immediately after stimulus onset in the 2 Hz frequency bin (Figure 4). Unlike for PLI, modulation of IPC was not clearly stronger in one frequency bin than in others. However, similar to the PLI results, sustained increases of synchronization were particularly observed in the 2 Hz frequency bin at 200 – 600ms post stimulus onset (Figure 7). Increases of IPC were followed by a particularly pronounced decrease of synchronization at 8 Hz 300 – 400 ms post stimulus presentation (Figure 7). Generally, initial increases of IPC were followed by later decreases across frequency bins (Figures 5 ans 6). We observed no differences in intra-brain phase coherence between individual and joint attention. Differences in both PLI and IPC between individual and joint attention were furthermore related with behavioral performance change (Figure 8). Adding measures of neural phase synchronization as predictors of behavioral change in visual search almost doubled the explanatory power compared to a regression that

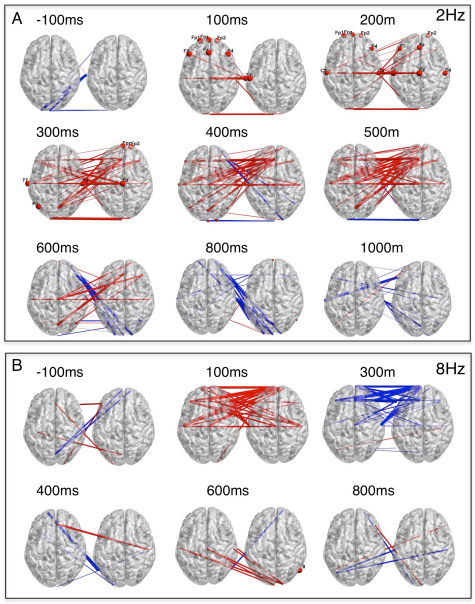



Figure 7. Time course of PLI and IPC at (A) 2 Hz and (B) 8 Hz. A. PLI and IPC values per electrode and electrode connection at 2 Hz. B. PLI and IPC values per electrode and electrode connection at 8 Hz. Nodes = PLI. Edges = IPC. Values are thresholded at > 2.5758 bootstrap ratios (approximating 99% CI). Significant nodes are labeled with the corresponding electrode name. Blue codes for negative values. Red codes for positive values.

only included the effect of session order (capturing the effect of training) as a predictor ($R^2$ adjusted 0.41 vs. $R^2$ adjusted 0.74, $F(4) = 6.55$, $p < 0.005$). In particular, brain scores obtained on IPC during the individual condition and brain scores obtained on PLI during the social condition uniquely predicted team efficiency score.

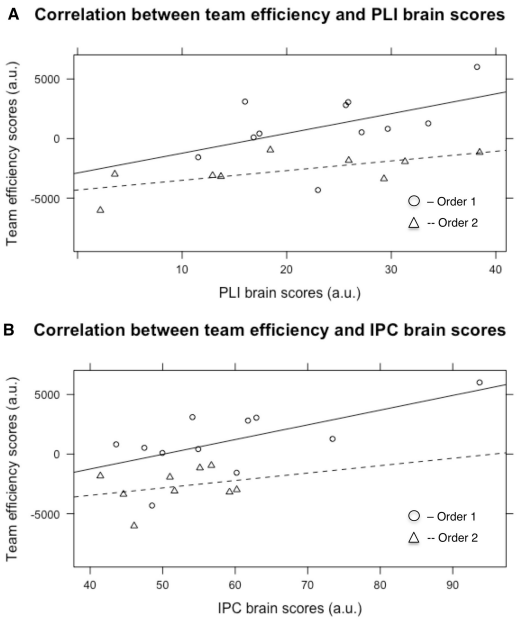



Figure 8. Correlation between team efficiency and phase synchronization (PLI and IPC). A. Correlation between team efficiency and PLI brain scores. B. Correlation between team efficiency and IPC brain scores. The difference score between brain scores estimated by nr-PLS in the social condition and brain scores estimated in the individual condition was correlated with team efficiency scores. Circles indicate the session order with the individual condition first (Order 1). Triangles indicate the session order with the social condition first (Order 2). Solid line = regression line for session Order 1. Dashed line = regression line for session Order 2.

**Conclusion.** In summary, we observed increased inter-brain phase synchronization and increased local phase synchronization for joint attention

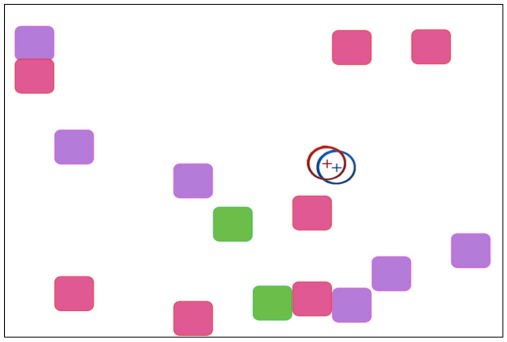
relative to individual attention during a visual search task. We interpreted these findings as neural substrates of social facilitation. Although local phase synchronization in one brain and inter-brain phase synchronization between brains may reflect similar cognitive processes, we found them to differ in explanatory power of behavioral performance. In our experimental setup session, order had a strong influence on behavioral performance and teamwork benefit and accounted for 50% of inter-dyad differences in benefit of working together. Remarkably, local and inter-brain phase synchronization combined, explained an additional 25% of inter-dyad differences in teamwork benefit. We conclude that inter-brain phase synchronization may be considered a useful tool in the study of neural team dynamics.

### 4.2 Study II: inter-brain phase synchronization during reciprocal and parallel interpersonal action coordination

**Szymanski, C.**, Brick, T. R., Perdikis, D., Müller, V., Karch, J., & Lindenberger, U. *On neural synchronization during interpersonal action coordination.* (under review entitled 'Neural Synchronization during Reciprocal and Parallel Dyadic Gaming' at *Frontiers in human neuroscience*).

**Background.** The recent *interactive turn* in social neuroscience has highlighted the importance of interpersonal interaction for the development and functioning of social cognition (De Jaegher, Di Paolo, & Gallagher, 2010; Gallotti & Frith, 2013; Schilbach et al., 2013; Sebanz et al., 2006). Studies using EEG hyperscanning have repeatedly revealed interpersonally synchronized patterns during interpersonal action coordination. Yet, consensus is lacking if this inter-brain synchronization is characteristic for social interaction in that it reflects shared cognitive action plans (Sänger et al., 2011) or if it mainly reflects the similarity of two person's motor output. To shed light on this core question of the current hyperscanning literature, we designed a novel computer-game paradigm to compare inter-brain phase synchronization during reciprocal, interactive interpersonal action coordination and during parallel, non-interactive interpersonal action coordination, preserving the same behavioral dynamics.

A



B

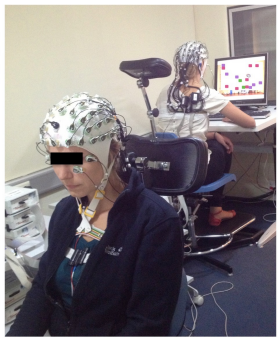


Figure 9.
A. Example display of the paradigm ‚Stay with me'.
B. Experimental set-up in the electro-magnetically shielded cabin.

**Aims.** We aimed to disentangle the relative impacts of (A) interpersonal interaction and (B) input/output similarity on inter-brain phase synchronization during interpersonal action coordination.

**Hypothesis.** From the current hyperscanning literature it is unclear if inter-brain phase synchronization solely reflects the similarity of perceptual input and motor output between two individuals or if it is further modulated by the presence of social interaction. We thus hypothesized that inter-brain phase synchronization would differentiate (A) between conditions that differ in output similarity and thus behavioral dynamics. We had no a-priori hypothesis on the sensitivity of inter-brain phase synchronization for social interaction and thus asked the research question if inter-brain phase synchronization would differentiate (B) between reciprocal and parallel interpersonal coordination.

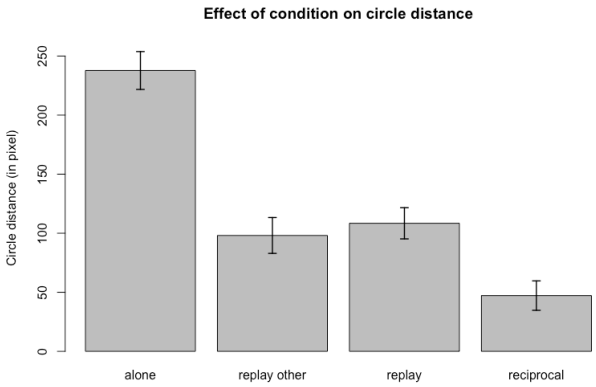



Figure 10. Results of a linear mixed model analysis for the effect of condition on circle distance.

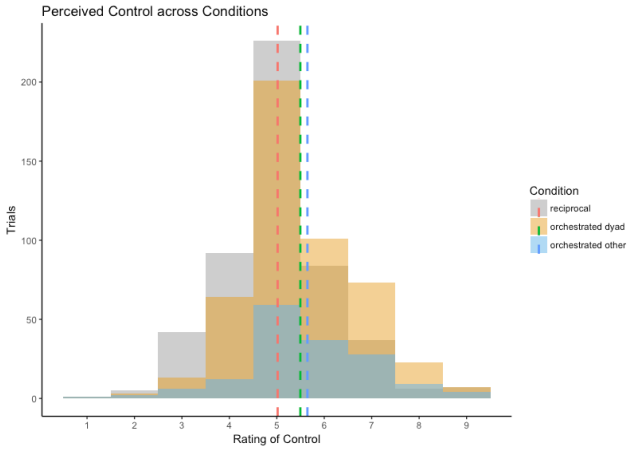



Figure 11. Histogram of the ratings of control across conditions registered at the end of each interactive trial. Dotted lines represent average rating per condition.

**Methods.** We had 13 male-male and 15 female-female dyads take part in this EEG hyperscanning study. We designed the novel interactive virtual game ‚Stay with me' to disentangle the relative impacts of interpersonal interaction and input/output similarity on inter-brain phase synchronization during action coordination (Figure 9). By recording behavioral patterns during reciprocal coordination and replaying these recorded patterns in later trials, this paradigm enabled us to compare reciprocal interactive coordination and parallel non-

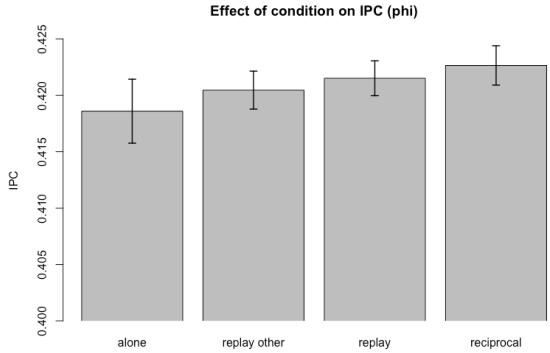



Figure 12. Results of a linear mixed model analysis for the effect of condition,on IPC in the phi range (8-12Hz, right centro-parietal electrode connections).

interactive coordination following the same behavioral dynamics. The participants' task was to navigate a virtual circle to (A) avoid collisions with moving virtual squares and (B) to align their circle with the second circle on the screen. Our four conditions differed with respect to the second circle's movements. While in *reciprocal* the second participant real-time controlled the second circle, in *replay* the second circle displayed the movement path of a circle recorded during a previous r*eciprocal* trial from the same dyad, in a identical square environment. In *replay other* the second circle was a replay of a recording during a *reciprocal* trial from a different dyad. In *alone,* there was no second circle and participants only had to avoid collisions with the squares (intra-personal coordination only). We calculated number of square collisions per trial as a measure of intra-personal coordination, circle distance in pixel per trial as a measure of interpersonal coordination and movement similarity and inter-brain phase coherence (IPC) as a measure of inter-brain phase synchronization. We used linear mixed models to assess differences in behavioral performance and IPC between conditions.

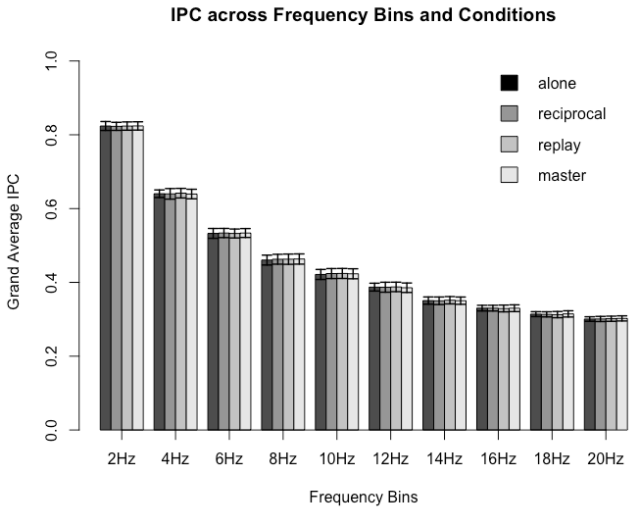



Figure 13. Grand average IPC values per frequency bin and condition.

**Results.** Analyses of our behavioral measures showed that behavioral dynamics followed the same general movement patterns in all four conditions with small differences between *reciprocal* and *replay* and larger differences between *reciprocal* and *alone (*Figure 10). Participants reported ‚mutual control' over circle movements for all conditions (Figure 11). We did not observe any differences in inter-brain phase synchonization between reciprocal interpersonal action coordination (*reciprocal*) and parallel interpersonal action coordination (*replay*) and thus our results give a negative answer to our second research question (B) for this study. We did however observe differences between *alone* and *reciprocal,* specifically in the alpha range in right centro-parietal electrode pairings and thus the results support our research hypothesis (A) for this study (Figure 12). Moreover, we observed a strong negative logarithmic relation between IPC and frequency band (Figure 13). On the behavioral level, subjects experienced reciprocal interpersonal coordination as well as parallel interpersonal coordination following the same behavioral dynamics as mutual teamwork (Figure 11). Additionally, our results on changes in coordination performance between playing alone and playing as a team replicated and extended an effect reported earlier in the literature (Bahrami et al. 2010). Due to the conceptualization of our paradigm, our task was more difficult in the three interpersonal conditions than in the *alone* condition. However, the degree of performance decrement was correlated with the skill difference between the two players in a dyad. The more two partners in a dyad differed in their coordination skills, the more the better player's performance deteriorated, while there was no systematic effect on the weaker player's performance change (Figure 14).

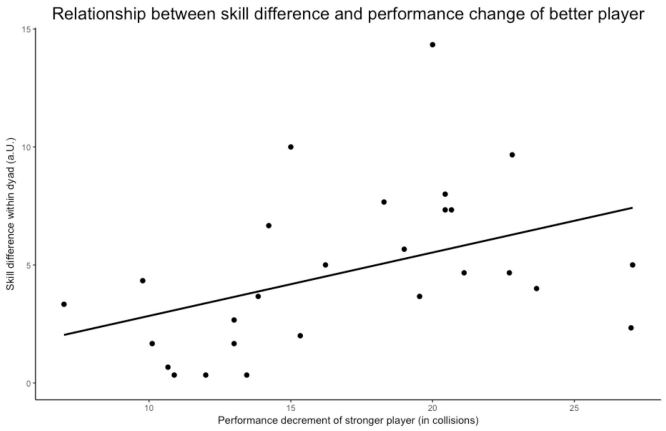



Figure 14. Effect of teamwork on coordination performance.

**Conclusion.** Inter-brain phase synchronization in the alpha range in right centro-parietal electrode pairings has previously been associated with interpersonal interactivity (Tognoli et al., 2007a). Our results instead suggest that this ‚phi' frequency and region may be particularly sensitive to the behavioral dynamics of an interaction. The results of our study suggest that interactive coordination is not systematically different, either experientially or neurally, from parallel coordination that is characterized by the same behvaioral dynamics. More generally, our evidence supports the idea that inter-brain phase synchronization may be seen as a

neural measure of behavioral dynamics that embodies characteristic (motor) information about an interaction.

### 4.3 Study III: methodological, prepatory study for Study IV

Kleinert, M.-L., **Szymanski**, **C**., & Müller, V. (2017). *Frequency-unspecific effects of θ-tACS on a visuo-spatial working memory task. Frontiers in human neuroscience. 11.* 367.

**Background.** To establish methodological expertise for Study III we sought to replicate a tACS study by Polania et al. (2012), who had used a stimulation protocol we intended to adjust for use in Study III. The authors had reported proof-of-concept for differential effects of tACS-induced frontoparietal theta synchronization vs. theta desynchronization. We indetend to replicate the results reported by Polania and colleagues: differential effects of in-phase vs. out-of-phase tACS at theta frequency over frontoparietal sites on working memory performances, particularly pronounced during high vs. low cognitive load. Additionally, we analyzed a potential impact of tACS onto EEG during rest with eyes closed, which we recorded before and after the stimulation.

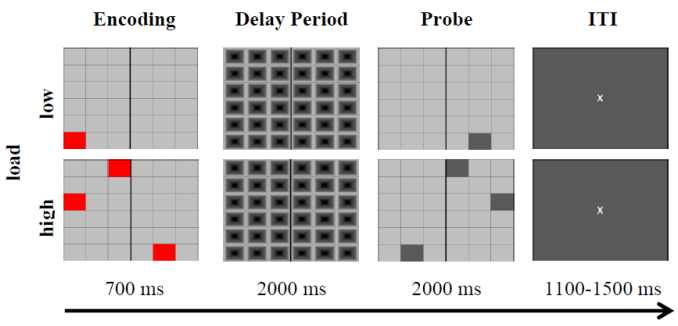



Figure 15. Representation of the delayed visuospatial match-to-sample task (MtS). Time course with corresponding stimulus material during low and high load, both match and non-match trials are displayed. ITI: Inter-trial interval. The MtS was adapted from Griesmayr et al. (2014) and modified respectively.

**Hypotheses.** We hypothesized that (a) in-phase stimulation of the fronto-parietal theta network would result in working memory performance enhancement, whereas we expected (b) anti-phase (180° relative phase angle) tACS to cause performance impairments. We further hypothesized that (c) this effect would be particularly pronounced during the high working memory load condition. Frequency-specificity of tACS (Feurra, Paulus, Walsh, & Kanai, 2011; for review see Herrmann, Rach, Neuling, & Struber, 2013), as well as after-effects of tACS (Neuling, Rach, & Herrmann, 2013; Veniero, Vossen, Gross, & Thut, 2015) have both been reported repeatedly in the literature and we thus hypothesized (d) post-stimulation resting EEG to be altered particularly in the theta range with respect to pre-stimulation resting EEG.

**Methods.** Eighteen healthy participants (20–29 years, mean = 25.20 years, SD = 2.96 years) performed a visuospatial delayed match-to-sample task (Figure

15) during tACS targeting frontoparietal sites (stimulation frequency = 5Hz; intensity = 1mA peak-to-peak; stimulation duration = 26min; target electrodes placed over F4 and P4, return electrode over Cz of the international 10 - 20 system). Over three experimental session separated by one week each, each participant underwent three different stimulation protocols (0° phase difference between frontocentral and parietocentral stimulation; 180° phase difference between frontocentral and parietocentral stimulation; sham stimulation). In each session participants performed the working memory task prior, during and after tACS. Additionally, resting EEG with eyes closed was recorded at the beginning of each experimental session and after tACS. A power analysis was performed on the EEG data for the delta (0.5-4Hz), theta (4-8Hz), alpha (8-12Hz) and beta (12-30Hz) frequency bands. In a further step, the difference between stimulation frequency (5Hz) and each participant's peak frequency within the theta range (Δθ) was analyzed to investigate shifts of individual theta peaks.

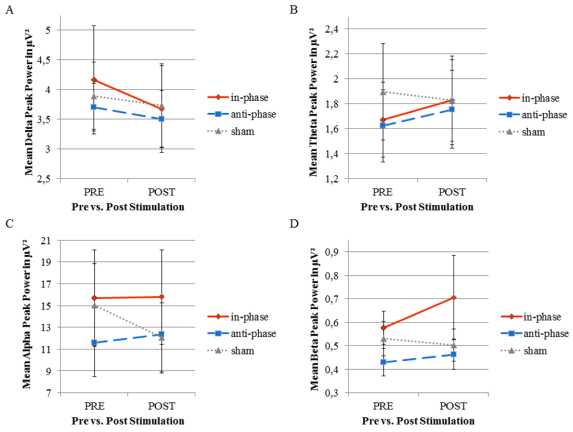



Figure 16. Mean peak power of resting EEG in the three stimulation conditions (in-phase, anti-phase, and sham) before and after stimulation for the delta, theta, alpha, and beta frequency bands. A. Delta frequency range (0.5–4 Hz). B. Theta frequency range (4–8 Hz). C. Alpha frequency range (8–12 Hz). D, Beta frequency range (12–30 Hz). Peak power (in µV ) was averaged across five electrodes within direct vicinity of the stimulation sites, i.e., Fz, F8, Pz, P8, and Oz. Standard error bars are displayed.

**Results.** We observed an effect of cognitive load (high/low) on log transformed reaction times as well as on accuracy but no effect of stimulation (in-phase/out-of-phase/sham) on either measure of behavioral working memory performance. Contrary to our experimental hypotheses, we observed no significant changes in the EEG power spectrum from pre-stimulation to post-stimulation in any of the analyzed frequency bands (see Figure 16) and consequently also no differences between the two stimulation conditions (in-phase and anti-phase). However, we detected a positive correlation between Δθ and log transformed reaction times during post-stimulation under the out-of-phase stimulation protocol ($r = 0.6$, $p < 0.01$). The closer participants' individual theta peak frequency was to the stimulation frequency of 5 Hz, the faster they responded during the working memory task.

**Conclusion.** In summary, we observed no tACS induced frequency-specific modulation of resting EEG after tACS as compared to resting EEG before tACS. Also, contrary to our hypothesis we did not detect any differential effect of in-phase vs. out-of-phase frontopariteal tACS at theta frequency on reaction time or accuracy in a visuospatial delayed match-to-sample task. However, the closer participants' individual theta peak frequency was to the stimulation frequency of 5 Hz during anti-phase tACS, the faster their behavioral responses during the post-stimulation task

session. This latter result is in line with findings in the literature that tACS modulates cortical oscillations in a frequency-specific manner. However, overall the results of study III suggest that the precise mechanisms of how tACS impacts neuronal circuits, in both a frequency-specific and a frequency-unspecific manner, are still not thouroughly understood.

### 4.4 Study IV: the relation between inter-brain phase synchronization and interpersonal action synchronization

**Szymanski**, C., Müller, V., Brick, T. R., von Oertzen, T., & Lindenberger, U. (2017). Hyper-Transcranial Alternating Current Stimulation: Experimental manipulation of inter-brain synchrony. *Frontiers in human neuroscience. 11.* 539.

Figure 17. Experimental set-up of the dyadic drumming paradigm. Participants drummed in symmetrical synchrony with each other or with a metronome while receiving hyper-tACS. They heard their digitalized drum beats via soundproof headphones.

**Background.** Evidence from the EEG hyperscanning literature suggests that the synchronization of oscillatory activity across brains may provide a mechanism for the temporal alignment of attention (Szymanski et al., 2017) and actions between two or more individuals (see for review and conceptualization e.g. Sänger et al., 2011). However, at the time hyperscanning studies had been of observational nature only and there had been no evidence for a causal link between interpersonally synchronized neural patterns and interpersonal action coordination performance.

**Aims.** The aim of this study was to provide a direct test of the hypothesis that inter-brain synchronization is causally associated with interpersonal action synchronization. We thus applied tACS simultaneously to two interacting individuals (hyper-tACS) who were asked to drum in synchrony at a set pace.

**Hypotheses.** We hypothesized that (A) same-phase-same-frequency stimulation would improve interpersonal action coordination, expressed as the degree of synchrony in dyadic drumming, relative to different-phase-different-frequency stimulation and sham stimulation and (B) that the degree of synchrony in metronome drumming would remain unaffected by hyper-tACS.

**Methods.** We had 38 female-female dyads perform a dyadic drumming paradigm previously established in our lab (Kleinspehn-Ammerlahn et al., 2011),

where participant's task was to drum a set pace either individually, with the other participant or with a metronome (Figure 17). We used a measure of behavioral drumming asynchrony established in the same preceding study and measured individual and dyadic preferred drumming tempi. Participants performed the dyadic drumming task over the course of three weeks under three different hyper-tACS stimulation conditions: same-phase-same-frequency (6Hz/6Hz; 0° phase offset); different-phase-different-frequency (5Hz/7Hz, 13° phase offset); sham. Apart from this manipulation the stimulation protocol was constant (stimulation intensity = 1mA peak-to-peak; stimulation duration = 25min; target electrodes placed over right F4 and P4, return electrode over Cz of the international 10 - 20 system). We assessed the impact of the different stimulation conditions on behavioral drumming performance using linear mixed models.

**Results.** Contrary to our guiding hypothesis, dyadic drumming synchronization performance decreased under both active hyper-tACS protocols as compared to sham stimulation (Figure 18 and Table 1). The results confirmed hypothesis (B) in that the degree of synchrony in metronome drumming was not systematically affected by hyper-tACS. We further observed no impact of hyper-tACS on individual preferred drumming tempi or on dyadic preferred drumming tempi (Figure 19). Of interest was our finding that dyadic preferred tempi were systematically faster then individual preferred tempi and that individual preferred tempi within a dyad further predicted the dyadic preferred tempo (Figure 19).

| Stimulation condition | Estimate | SE | DF | T-value | Pr(>\|t\|) |
|---|---|---|---|---|---|
| **Pre** | 1574.16 | 60.53 | 46 | 26.007 | < 0.0001 |
| **S Stim** | -90.11 | 22.23 | 4846 | -4.054 | < 0.0001 |
| **SF Stim** | 19.28 | 22.10 | 4856 | 0.872 | = 0.383 |
| **DF Stim** | -31.19 | 21.60 | 4868 | -1.444 | = 0.149 |
| **S Post** | -175.70 | 31.00 | 4865 | -5.668 | < 0.0001 |
| **SF Post** | -106.96 | 31.21 | 4863 | -3.427 | < 0.0001 |
| **DF Post** | -86.36 | 30.43 | 4858 | -2.838 | < 0.005 |

Table 1. Fixed effects estimated with linear mixed models grouped by dyad for dyadic asynchrony scores. Stimulation conditions: Pre = pre, S Stim = sham stimulation, SF Stim = same-phase-same-frequency stimulation, DF Stim = different-phase-different-frequency stimulation, S Post = sham post, SF Post = same-phase-same-frequency post, DF Post = different-phase-different-frequency post.

**Conclusion.** In this proof-of-concept study we presented evidence that active hyper-tACS in the theta range over right frontocentral and parietocentral sites affected dyadic drumming synchronization specifically, while metronome drumming synchronization as well as drumming tempo were unaffected by hyper-tACS. We discussed limitations of our stimulation setup that might not have been adequately optimized to entrain neural oscillations across brains in a same-phase-same-frequency manner and instead both active hyper-tACS conditions might have desynchronized natural inter-brain phase synchronization.

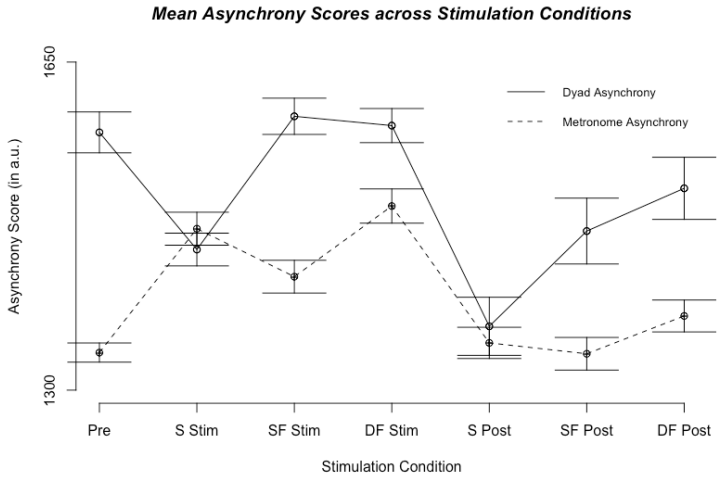



Figure 18. Mean dyadic asynchrony scores and metronome asynchrony scores for all experimental conditions. Stimulation conditions: Pre = pre, S Stim = sham stimulation, SF Stim = same-phase-same-frequency stimulation, DF Stim = different-phase-different-frequency stimulation, S Post = sham post, SF Post = same-phase-same-frequency post, DF Post = different-phase-different-frequency post. Standard errors are indicated by horizontal lines.

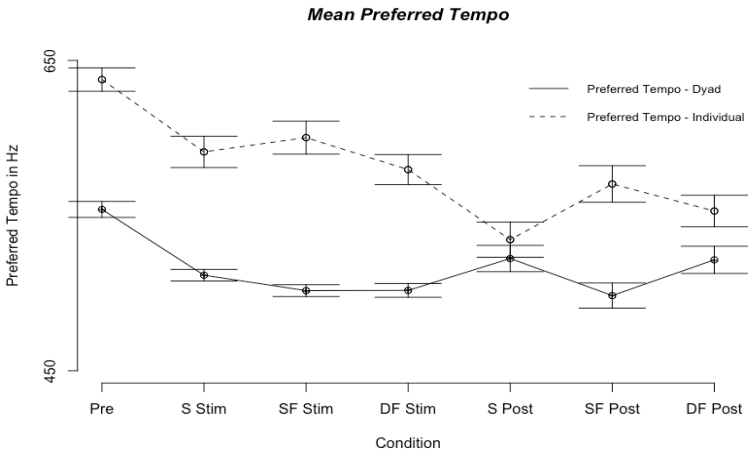



Figure 19. Mean preferred tempo for all experimental conditions. Stimulation conditions: Pre = pre, S Stim = sham stimulation, SF Stim = same-phase-same-frequency stimulation, DF Stim = different-phase-different-frequency stimulation, S Post = sham post, SF Post = same-phase-same-frequency post, DF Post = different-phase-different-frequency post. Standard errors are indicated by horizontal lines.

## 5 General discussion

This dissertation aims to advance the understanding of the role of inter-brain synchronization in social interaction and interpersonal action coordination by addressing two main research questions: (1) Does inter-brain phase synchronization reflect characteristics of interpersonal action coordination other than input/output similarity? (2) How is inter-brain phase synchronization related to interpersonal action coordination performance? In the following discussion, I will first summarize the results of each empirical study and set them in the context of these two overarching research questions. Second, I will analyze the relation between inter-brain synchronized patterns, social interaction, and behavioral dynamics and point out how diverging and under-specified theoretical models of social interaction cause dissent about the functional role of inter-brain patterns. Third, I will propose a working definition of social interaction and its core mechanisms, namely attention, prediction and reaction. Fourth, I will advocate the use of a clear definition of social

interaction, which builds on existing theoretical frameworks of interpersonal action coordination. I will conclude this dissertation with the outlook to stop isolating inherent aspects of social interaction, such as synchronized actions, from ‚true social interaction' and instead to focus on the relative influence of attentive, predictive and reactive mechanisms on inter-brain synchronization and associated behavioral dynamics.

## 5.1 Empirical studies

### 5.1.1 Study I

Study I focused on a core aspect of interpersonal action coordination, namely joint attention. The specific research questions of Study I were as follows:

(A) Is inter-brain phase synchronization sensitive to the presence of ‚the other', thus does inter-brain phase synchronization differ between individual and joint attention under identical perceptual input?

(B) Do between-pair differences in inter-brain phase synchronization during joint attention correlate with between-pair differences in behavioral performance on a teamwork task?

The results of Study I provided positive answers to both research questions. IPC differed between individual and joint attention and the mean size of this difference correlated with mean change in behavioral performance from individual enumeration search to team enumeration search.

The paradigm (visual search enumeration) was chosen specifically to overcome limitations of earlier EEG hyperscanning studies, in that it kept perceptual input and motor output stable between the two conditions of interest (individual and social condition). This was achieved by analyzing only the first second of EEG data after stimulus presentation, when subjects were engaged in individual or joint visual attention, but did not yet perform any motor actions such as button presses. This analyzed period was however the beginning of a visual search trial and thus the paradigm allowed studying the relation between inter-brain synchronized patterns during an initial attention period and the behavioral response several seconds later. Besides inter-brain phase synchronization (measured as IPC), also local within-brain synchronization (measured as PLI) changed from individual attention to joined attention. For PLI, this increase from individual to joint attention was most pronounced in the 2Hz frequency bin at frontal, central and parietal electrode sites 0-400ms post-stimulus onset, with smaller increases and decreases with different timings also in other frequency bins. IPC mirrored the strong increase in PLI in fronto-centro and fronto-pariteal electrode sites in the 2Hz frequency bin, but it appeared slightly later in time (200 - 600ms post-stimulus onset). If one assumed that this increase in IPC in the social condition was due to greater similarity in motor output, more similar eye movement patterns during joint as opposed to individual search would be the only explanation. Alternatively, social facilitation (probably via heightened individual attention) might have driven this increase in inter-brain synchronized patterns. This explanantion is supported by the finding that differences in both PLI and IPC between individual and joint attention were correlated with behavioral performance changes from individual to teamwork.

Measures of neural phase synchronization as predictors of behavioral change in visual search accounted for roughly 50% of explanatory power in the statistical model. This result may be seen as supporting the aforementioned interpretation as heightened (joint) attention would likely result in better (team) performance.

Taken together, Study I yielded positive answers to research question (1). Inter-brain synchronization not only reflects input/output similarity but is sensitive to social context. The results also inform the main research question (2) in that they show a correlation between the change in inter-brain synchronization associated with social context and performance benefits during social context.

### 5.1.2 Study II

Study II compared inter-brain phase synchronization across reciprocal interpersonal action coordination, parallel interpersonal action coordination following the same behavioral dynamics and intra-personal action coordination with different behavioral dynamics.

Study II addressed the following specific research questions:

(A) Does inter-brain phase synchronization differentiate between reciprocal and parallel coordination preserving the same behavioral dynamics, thus is it sensitive to the presence of real-time interaction?

(B) Does inter-brain phase synchronization differentiate between conditions that differ in their behavioral dynamics, thus is it sensitive to differences in motor output similarity?

The results give a negative answer to research question (A). Contrary to expectations, we found no evidence that inter-brain phase synchronization differs between reciprocal and parallel interpersonal action coordination in the paradigm used in this study. This negative result is consistent with the notion that inter-brain phase synchronization is not sensitive to the presence of interaction as such. As the absence of evidence does not prove the absence of an effect, one cannot interpret this negative result definitely. However, given that the study was set up to compare two conditions that did not differ in input/output similarity and in their behavioral dynamics but only in the presence of interaction, this negative finding should serve as a cautionary note, that the presence of interaction as such is at least not a necessary condition for the presence/increase of inter-brain phase synchronization.

The results provided support for research question (B): inter-brain phase synchronization is sensitive to differences in input/output similarity and thus to differences in behavioral dynamics. We observed differences in IPC between reciprocal interpersonal coordination and intrapersonal coordination that was modulated by coordination performance (measured as circle distance). Interestingly we also observed a trend suggesting that this difference does not reflect the binary variable ‚interpersonal'/'intrapersonal' but that it rather reflects increasing differences in behavioral dynamics (from the smallest difference in *reciprocal coordination* to *parallel coordination same dyad* to *parallel coordination different dyad* to the biggest difference in *intrapersonal coordination only).* Also, participants did not report any conscious awareness of the parallel coordination manipulation;

instead they perceived both reciprocal and parallel coordination as mutually controlled teamwork.

Contrary to the results of Study I, the results of Study II give a negative answer to the main research question (1). Instead they suggest that the presence of interaction does not impact inter-brain phase synchronization, but rather that differences in behavioral dynamics are associated with corresponding differences in inter-brain phase synchronization. Along this line, the results of Study II also inform the main research question (2): coordination performance, in this case equivalent to similarity of behavioral dynamics, is reflected in inter-brain phase synchronization.

### 5.1.3 Study III

Study III served as a preparatory study to Study IV to establish the tACS methodology in the lab. Study III was set up to replicate results reported by Polania and colleagues (2012), namely differential effects of in-phase vs. out-of-phase tACS at theta frequency over frontoparietal sites on working memory performances and did not adress the main research questions (1) and (2).

Study III instead addressed the following three specific research questions:

(A) Does in-phase stimulation of the fronto-parietal theta network result in working memory performance enhancement?

(B) Does anti-phase (180° relative phase angle) tACS cause performance impairments?

(C) Is this effect particularly pronounced during the high working memory load condition?

The results of Study III were mixed with regard to research question (A). The closer participants' individual theta peak frequency was to the stimulation frequency of 5 Hz, the faster they responded during the working memory task. However, we observed no overall performance differences between in-phase and anti-phase tACS and thus the results did not support research questions (B) and (C). TACS is widely considered a valuable method in cognitive neuroscience (Herrmann et al., 2013) and its frequency-specific impact on neural oscillations has been repeatdely reported (e.g., Zaehle, Rach, & Herrmann, 2010). However, the absence of frequency-specific effects on neural oscillations has also been reported (Brignani, Ruzzoli, Mauri, & Miniussi, 2013; for review see Veniero et al., 2015). Taken together, the results of Study III reflect the ongoing debate on how tACS precisely entrains intrinsic neural oscillations (Thut, Schyns, & Gross, 2011; Underwood, 2016) and emphasize that this modulation is not simple and one-dimensional.

### 5.1.4 Study IV

Study IV experimentally manipulated inter-brain phase synchronized patterns and studied subsequent effects on behavioral interpersonal synchronization

performance during dyadic drumming. Study IV addressed the following research questions:

(A) Does same-phase-same-frequency hyper-tACS improve dyadic drumming synchronization, while different-phase-different-frequency hyper-tACS deteriorates dyadic drumming synchronization?

(B) Does metronome drumming synchronization as well as individual and dyadic preferred drumming tempo remain unaffected by hyper-tACS?

The results yielded a complex answer to research question (A) and a positive answer to research question (B). Metronome drumming synchronization, individual and dyadic preferred tempi under sham stimulation were not systematically altered by either same-phase-same-frequency hyper-tACS or by different-phase-different-frequency hyper-tACS. In contrast, dyadic drumming synchronization was systematically affected by hyper-tACS in that dyadic synchronization performance deteriorated under both active hyper-tACS protocols. These results suggest that inter-brain phase synchronization is directly related to interpersonal action coordination performance; however, the characteristics of this relationship and the precise frequency-specific and frequency-unspecific effects of tACS remain to be investigated further.

Very recently, Novembre and colleagues applied hyper-tACS with a different stimulation protocol (Novembre et al., 2017). The authors reported that in-phase hyper-tACS applied over the left motor cortex at 20Hz facilitated synchronization performance in a dyadic tapping paradigm, while anti-phase hyper-tACS with an otherwise identical stimulation protocol degraded interpersonal synchronization performance. Stimulation at delta or alpha frequencies had no effect on performance. These results support the interpretation of empirical Study IV that inter-brain phase synchronization is directly related to interpersonal action coordination performance. Hyper-tACS appears to be a useful tool to investigate the interplay between inter-brain synchronized patterns and interpersonal action coordination in more detail.

Taken together, the results of Study IV suggest the following answer to the main research question (2): inter-brain synchronized neural patterns appear to be specifically related to interpersonal synchronization performance. However, inter-brain synchronized patterns likely extend over different brain regions and different frequency bands, which are each potentially related to different aspects of interpersonally coordinated actions.

To summarize, the empirical studies give differential answers to the two major research questions. Study I shows that social interaction in the form of joint attention influences inter brain phase synchronization. In contrast, Study II shows no impact of reciprocal interaction on inter-brain synchronized patterns when controlling for synchronized motor output. Study IV again suggests a relation between social interaction and inter-brain synchronization, in that only interactive synchronization performance was impacted by experimental manipulation of inter-brain synchronization. So how to interpret the overall contribution of this dissertation to our understanding of the functional role of inter-brain synchronized patterns? A quote by Liu and Pelowski seems poignant: “Although recent hyperscanning studies

have revealed intrigung synchronization, it remains difficult to explain exactly how and why inter-brain synchronization occurs" (T. Liu & Pelowski, 2014a, p. 1). With this dissertation I initially intended to provide two main contributions to the study of inter-brain synchronized patterns and their relation to social interaction and interpersonal action coordination: First, I thought to test the relation of inter-brain synchronized patterns and social interaction, by using experimental control conditions that keep similarity of perceptual input and motor output stable while varying social context only. Second, I aimed to investigate the relation between inter-brain synchronized patterns and interpersonal action coordination by providing a direct test of the hypothesis that inter-brain phase synchronization is related to interpersonal synchronization performance. In the following section, I will provide an analysis of the relation of inter-brain synchronized patterns and synchronized behavioral dynamics.

### 5.2 Behavioral dynamics and inter-brain synchronized patterns

The strict separation of synchronized behavioral dynamics as a confounding factor that obscures the contribution of ‚real interaction' to inter-brain synchronization stands in stark contrast to an influential framework proposed by Scott Kelso that defines synchronized behavioral dynamics as a defining feature of social interaction. The ‚theory of dynamic patterns' (Kelso, 1997) proposes that behavioral patterns are a result of the self-organized coordination of distinct, yet mutually coupled, systems made up of muscles or neurons. From this perspective, two interacting individuals become coupled through their behavioral interaction (Kelso, Dumas, & Tognoli, 2013). The resulting dynamics that emerge from this interaction, the *coordination dynamics,* are at the same time constitutive of the coordination itself. In light of this framework, the behavioral dynamics of an interpersonally coordinated action are no cofounding, but a core factor of an interaction. Indeed, studies comparing *intra*-personal coordination to *inter*personal coordination showed that both cases rely on the same dynamical organizing principles (Schmidt & Richardson, 2008) in the sense that the limbs of two different persons, just as the different limbs of one person, form a coupled unit. Behavioral studies repeatedly demonstrated emergent coordination dynamics in the motor behavior of two interacting participants e.g. when rocking in chairs or tapping their fingers (Konvalinka, Vuust, Roepstorff, & Frith, 2010; Richardson, Marsh, Isenhower, Goodman, & Schmidt, 2007) and developmental studies further highlighted the role of reciprocal interaction for the development of social cognition as such (Carpendale & Lewis, 2004). Auvray and Rohde have called to connect these behavioral phenomena to neural processing: "One major open question for interactionist research on social cognition is the study of how the underlying processes are neurally implemented." (Auvray & Rohde, 2012, p. 11) With a suggestion from Schmidt and Richardson in mind, according to whom the organizing principles predicted by the coordination dynamics approach "can operate in neurally-based behavioral oscillatory systems that are coupled by perceptual information and, consequently, that these principles represent a universal self-organizing strategy that occurs at multiple scales of nature" (Schmidt & Richardson, 2008, p.8), one almost inevitably thinks of *hyperscanning* as a tool with the ability to shed light on the question of how neural mechanisms relate to coordination dynamics in social

interaction (see e.g. De Jaegher, Di Paolo, & Adolphs, 2016; Kelso et al., 2013; Konvalinka & Roepstorff, 2012). Although the theoretical framework is popular among interactionist researchers, it is still not widely considered in the social neuroscience and hyperscanning literature. Specifically, „the value of a new framework in allowing us to formulate questions in a different vocabulary“ (Stewart, 2010, p.35), has been largely disregarded in the field of hyperscanning, where synchronized behavioral dynamics are still seen as something that needs to be controlled for in the study of social interaction. But if the field of hyperscanning, including the empirical studies in this dissertation, aims to ‚control for' major aspects of social interaction, how will it uncover the influence of social interaction on inter-brain synchronized patterns?

### 5.3 The lack of a definitional model of social interaction in the field of hyperscanning

In 2015 Hari and colleagues outlined specific requirements for control conditions to address “a major concern in the interpretation of hyperscanning data [, which] is the inability to disentangle the correlations evoked by social interaction from other possible common sources between the subjects“. (Hari et al., 2015, p. 14). The authors specify that (A) temporal correlations in brain signals (associated with synchronized movements), (B) predictive brain activations (reflecting dynamic asymmetry between differing sociocognitve roles) and (C) social facilitation “likely influences brain responses to stimuli or tasks that are not even related to the other” (Hari et al., 2015, p.14) and recommend to disentangle the multiple sources that contribute to interindividual synchrony and alignment: monitoring, predicting, reacting. Studies comparing competition to cooperation have yet come closest to providing individual control conditions. But competition and cooperation also constitute two different social contexts with differential demands for predictive brain activity. Thus the comparison cooperation/competition does not satisfy the threefold control (temporal correlations, predictive brain activation, social facilitation) proposed by Hari and colleagues (Hari et al., 2015). The same critique applies to studies focusing on interpersonal communication, which have repeatedly shown speaker-listener coupling (Kawasaki et al., 2013; Kuhlen et al., 2012; Stephens et al., 2010) that was linked to story comprehension (Stephens et al., 2010). Thus, according to Hari and colleagues these findings suggest that predictive brain activity and sociocognitve roles indeed influence inter-brain synchronization, while 'the other' or social interaction might have no effect. The implicit quest in the literature on two-person neuroscience is generally one for the neural mechanism underlying social interaction: „An important step forward in social neuroscience is the development of paradigms allowing for the study of such true, real-time social interactions“ (Singer, 2012, p. 9). „Ultimately, one would like to study people who are in real social interaction.“ (Hari et al., 2015, p. 8).

But what is *real social interaction*? The term is rarely explicitly defined in the hyperscanning literature, and researchers with differing definitions of social interaction have trouble in agreeing on what role inter-brain synchronized patterns have been shown to play in social interaction or interpersonal action coordination. The definition that „joint action can be regarded as any form of social interaction

whereby two or more individuals coordinate their actions in space and time to bring about a change in the environment“ (Sebanz et al., 2006, p.70) is widely accepted in the literature, while no definition of social interaction is widely used and clearly cited. For example in ‚Centrality of Social Interaction in Human Brain Function‘ Hari and colleagues (2015) give no clear definition of their understanding of social interaction. Schilbach has called to investigate “social interaction and its relationship to social cognitive abilities in more ecologically valid ways” (Schilbach et al., 2013, p. 413), but does not provide a definition of social interaction. Konvalinka and Roepstorff suggest social online interactions to involve “real-time coordination of actions, goals, and intentions. After all, social interaction is a largely dynamic process, which is about much more than observing and imitating.” (Konvalinka & Roepstorff, 2012, p. 2) but give no clear definition of social interaction. Liu and Pelowski (T. Liu & Pelowski, 2014b) suggest categorizing social interaction into two types - concurrent and turn-based interaction - and refer to a definition of interaction by Johnson and Johnson (Johnson & Johnson, 2005): “Individual’s simultaneous or sequential actions that affect the immediate and future outcomes of the other individuals involved in the situation”. In contrast to the definition of interaction in the Cambridge dictionary: “occasion when two or more people or things communicate with or react to each other”, the definition by Johnson and Johnson does not entail reciprocity/mutuality. Reciprocity however, “where the reactions of one subject are the stimuli for the other subject, and vice versa.” (Hari et al., 2015, p. 7), has been highlighted as an important feature of social interaction (de Bruin, van Elk, & Newen, 2012) and is probably at the core of what many authors allude to when contrasting online, real-time interaction with offline interactions (de Bruin et al., 2012; Gallotti & Frith, 2013; Konvalinka and Roepstorff, 2012; Pfeiffer et al., 2014; Schilbach et al., 2013).

### 5.4 A working definition for social interaction and its relation to interpersonal action coordination

Building on earlier work in joint action (Vesper, Butterfill, Knoblich, & Sebanz, 2010), Peter Keller suggested a model for the factors influencing interpersonal action coordination (see e.g. Keller, Novembre, & Hove, 2014) At the level of cognitive-motor skills these namely encompass attention, anticipation and adaption. I propose to combine this model with the dynamical patterns theory by Scott Kelso to define social interaction as *the actions of multiple agents that involve attentive, predictive and reactive qualities towards each other.* Thus, the behavioral dynamics of these actions make up a fundamental part of any social interaction and social interaction cannot be studied without studying behavioral dynamics. Importantly for the study of inter-brain synchronized patterns, it is impossible to disentangle synchronized actions and social interaction by construing two conditions that are identical in their behavioral dynamics, but differ in the presence or absence of social interaction. The very presence or absence of social interaction necessarily changes the behavioral dynamics, as this is what social interaction is: reciprocal actions. This definition also implies that social interaction and interpersonal action coordination are distinct phenomena.

### 5.5 Dissociating social interaction and interpersonal action coordination

Consider a moving conveyor belt in a warehouse wherein one worker loads boxes onto the belt, and another removes them at the far end, with the belt moving one step each time a box is loaded or removed. Successful coordination here implies that boxes do not fall off the end of the belt, neither do they pile up at its beginning. This coordination can be considered an interpersonally coordinated action involving social interaction if each worker adjusts their speed to the speed of the other, thus attends to, and predicts the other's speed and reacts to it. However, it is also possible that the worker loading boxes is unaware of the worker removing them and vice versa; they may instead simply be unloading/removing as fast as possible, neither predicting the other worker's speed, nor reacting to it. Still, this may look like successful interpersonally coordinated action, if the removing worker's speed happens to correspond to the loading workers speed. Also, imagine a case of planned or orchestrated interpersonal coordination, where both workers have received a plan of how fast to work. There need not be any social interaction between the two, but if both independently adhere to the same plan their coordination will nevertheless appear smooth and flawless. When two agents form ‚a coupled unit', (Schmidt & Richardson, 2008) thus both attend, predict and react to each other's actions, they will adopt their behavior upon perturbation (a sudden change in the mechanism of the moving belt, e.g. moving two steps each time a box is loaded) with respect to the other's actions, but would not do so in the absence of social interaction (= do not form ‚a coupled unit', but act independent of one another).

Consider again the conveyor belt. This time both agents attend, predict and react to each other's actions. However, one agent just started working in the factory and although he predicts when to load the next box on the belt based on the other worker's speed, his predictions do not match reality, he reacts too slowly and to a neutral observer the interaction between the two workers appears entirely uncoordinated.

Follwing the defintion provided in this dissertation social interaction is neutral with regard to the action outcome. If two agents' actions display reactive, predictive and attentive qualities towards one other, these agents are interacting socially, irrespective of their intentions (to interact) and the action outcome. Interpersonal action coordination on the other hand entails a notion of performance as it is seen as directed towards a (shared) goal. In an attempt to spell out a minimalistic definition of joint action Butterfill keeps the definition devoid of intentions or representations but still included a collective goal: "A joint action is an event with two or more agents where the actions grounding that event have a collective goal." (Butterfill, forthcoming, p.15). Some special forms of interpersonal action coordination, e.g entrainment, may take place unconsciously (Richardson, Marsh, & Schmidt, 2005) and thus do not rely on a collective goal. Nevertheless, also in these cases there is a clear notion of an ideal action outcome (e.g. the ideal outcome for entrainement is synchronized movement).

Thus, the definition of social interaction as the actions of multiple agents that involve attentive, predictive and reactive qualities towards each other pays respect to the

concept of reciprocity, ‚real-time', online social interaction (de Bruin et al., 2012) and at the same time distinguishes social interaction from interpersonal action coordination in that the latter involves a collective goal that defines an optimal action outcome.

### 5.6 Social interaction and inter-brain synchronized patterns

Sänger, Müller and Lindenberger (2011) proposed a conceptual framework on inter-brain synchronization in interpersonal action coordination. They proposed a forward model for interpersonal action coordination, where action intentions are derived from a joint goal and represenations of the actions to be performed by oneself and one's partner(s) are formed and compared to action effects. This model is an extension of the forward model for individual motor control (introduced by Wolpert, Ghahramani, & Jordan, 1995). Sänger, Müller and Lindenberger (2011) essentially suggest that both agents represent their own actions as a first layer of forward models and their partner's actions as a second layer of forward models. Thus, both agents activate corresponding brain regions due to their corresponding mental models, which results in inter-brain synchronization. The authors further suggest that, particularly in individuals who are highly skilled in their interactive task, a third layer may emerge where joint intentions and joint actions are represented detached from the agents' individual contributions. In this context Butterfill (forthcoming) has argued that there are different types of joint action, some of which demand invoking intentions, while others are devoid of intentions. Also Sänger and colleagues point out that it is currently unclear how joint intentions are formed and how individual intentions relate to them and that it is thus questionable how much the abstract notions of (joint) goals and (joint) intentions advance our understading of the concrete mechansism and functions of inter-brain synchronization (Sänger et al., 2011). Taken together, at the core of the forward model for action coordination lays the idea that not only one's own, but also one's partners actions are predicted and their effects on the environment are monitored. The subsequent adjustment of predictions and actions based on this sensory feedback is not explicitly spelled out in the model, but follows implicitly. Thus, attentive, predictive and reactive mechanisms with regard to others' actions also lie at the core of this theoretical model.

In order to demystify which different sources of modulations of brain activity need to be disentangled (compare Hari et al., 2015) for a better understanding of the functional role of inter-brain synchronized patterns for social interaction and interpersonal action coordination, I suggest to construe paradigms that focus on the concrete roles of attentive, predictive and reactive mechanisms. This approach is intended to open avenues. Certainly other cognitive mechanisms may be important in social interaction. In order to design future hyperscanning studies one should first spell out how one defines social interaction and which mechanisms supposedly impact it to then study these mechanisms' impacts on inter-brain synchronized patterns. Rather than aiming to keep input/output stable while varying social context, one should thus explore how attentive, predictive and reactive mechanisms impact inter-brain synchronized patterns and their corresponding actions.

In light of this perspective shift, the two major research questions of this dissertation need to be reformulated:

(1) How do the different cognitive mechanisms underlying social interaction (e.g. attention, prediction and reaction) influence inter-brain phase synchronization?

(2) How is inter-brain phase synchronization related to coordination dynamics and in particular to interpersonal action coordination performance?

## 6 Conclusion and outlook

In the final section of this synopsis, I will discuss the results of the empirical studies in the context of these two reformulated questions and propose possible avenues for future research. Study I on joint attention focused on the mechanism of attention. In Study I attention was varied (individual vs. joint), while predictive and reactive mechanisms played a smaller role during the time period studied in the visual search task. The results suggest that heightened attention (through social facilitation) is reflected in increased inter-brain synchronization. Future studies may investigate if heightened attention in one participant alone can drive increases in inter-brain synchronization. Asymmetries in inter-brain synchronization have repeatedly been observed for different sociocognitive roles (see e.g. Jiang et al., 2015; Konvalinka et al., 2014; Sänger et al., 2013). Thus, inter-brain synchronization may reflect the extent of cognitive commonalities between participants. Study II intended to construe an experimental condition that kept input/output similarity stable, but only varied social interaction. This was operationalized by what we called ‚parallel coordination without interaction'. Here, a recording of an earlier trial was replayed to the participants and hence there was no reaction (from the recording) or interaction between the participants at the moment of replay. We did not observe any differences in inter-brain synchronization between ‚reciprocal' (real-time, social interaction) and ‚replay' (recording) coordination, but we observed differences between ‚reciprocal' and ‚alone', when subjects merely coordinated their actions with the environment. In the latter comparison also input/output similarity differed much more. One would thus be inclined to conclude that while input/output similarity influences inter-brain synchronized patterns, social interaction does not do so. However, considering the definition of social interaction provided above, this interpretation changes drastically. The recording contained actions with attentive, predictive and reactive qualities. At the moment of recording, the environment was identical to the environment at the moment of replay and so was in many cases the subject's circle position. The results showed that subjects experienced to mutually control their movement path with the replay - potentially because at the moment of replay, the replay oftentimes correctly ‚predicted' the subject's current position and ‚reacted' to this position, as the subject had been in the same place during the moment of recording. As mentioned above, we observed no difference in inter-brain synchronization between ‚reciprocal' (online social interaction that involved attentive, predictive and reactive qualities) and ‚replay' (offline social interaction that, through the replay-trick, involved attentive, predictive and reactive qualities). Thus, it is likely not the often stressed real-timeness that is truly essential in social interaction (Hari et al., 2015; Konvalinka & Roepstorff, 2012; T. Liu & Pelowski, 2014a; Schilbach et al., 2013), but mechanisms of attention,

prediction and reaction that usually happen during such real-time interactions (Keller et al., 2014; Sebanz & Knoblich, 2009).

Study IV directly tested the relation between changes in inter-brain synchronization and changes in drumming synchronization performance. According to the framework of attention, prediction and reaction, this study tested the effect of experimental manipulation of inter-brain synchronization on attentive, predictive and reactive qualities in action synchronization.

Dyadic synchronization and metronome synchronization essentially differ in their demand for prediction and reaction. Metronome beat is stable and drumming with attentive and predictive qualities yields metronome synchronicity. Human beat on the other hand varies slightly (Smit, Linkenkaer-Hansen, & de Geus, 2013). In addition to constant updating of predictive mechanisms, reactive mechanisms are thus necessary to achieve dyadic synchronicity (Pecenka & Keller, 2011). Interestingly, hyper-tACS only impacted dyadic synchronization performance, suggesting that inter-brain synchronized patterns reflect the updating of predictive qualities and the presence of reactive qualities during interpersonal action coordination. However, the results of this study further suggest this relation to be anything but simple, as dyadic synchronization performance deteriorated in cases of both in-phase and out-of-phase hyper-tACS. Novembre and colleagues have recently performed an almost identical study that differed with respect to the chosen stimulation frequency and stimulation site (Novembre et al., 2017). While in our study we targeted fronto-parietal sites in the right hemisphere at theta frequency, Novembre and colleagues targeted motor areas in the left hemisphere at varying frequencies and reported an effect of synchronization facilitation exclusive to in-phase stimulation at 20Hz. Potentially, inter-brain synchronization across different regions and different frequencies may reflect different aspects of social interaction. Potentially, inter-brain synchronization at 20Hz in contralateral motor areas may reflect commonalities in two individual's action prediction mechanisms, while inter-brain synchronization at 6Hz in right centro-pariteal areas may reflect commonalities in reactive mechanisms. Also, some mechanisms may be more general for social interaction (and are thus facilitated by stimulation), while others may be more dyad-specific (and thus deteriorate upon unpersonalized manipulation). Investigating the different frequencies and regions of inter-brain synchronization in more detail and disentangling their contributions to attention, prediction and reaction remains one challenge for future research in the field of hyperscanning. Future studies in the field of hyperscanning and social interaction may thus start by investigating and disentangling the impact of reactive and predictive mechanisms on inter-brain synchronized patterns.

Importantly for this endeavor, one may turn to consider interaction a *gradual* rather than a binary quality. For example there may be cases of *one-way interaction*, a situation in which one agent's actions display attentive, predictive and reactive qualities, while a second agent is not aware of any interaction and focuses only on his own actions, which thus display only attentive and predictive qualities. Is such one-way social interaction characterized by asymmetries in inter-brain synchronized patterns? In many natural social interactions interacting agents display differential degrees of attentive, predictive and reactive qualities. For example the individual capacity for reaction has been linked to dyad performance (Pecenka & Keller,

2011). May asymmetries in inter-brain synchronized patterns quantify such differential engagement of cognitive mechanisms needed for successful interpersonal action coordination?

Actions that involve heightened attention due to social facilitation may serve as an example here. Studying the relation between the extend of attention/prediction/reaction displayed by two agents and the success of their interpersonal action coordination performance may be of particular interest to our understanding of teamwork and the concept of leadership. Are there for example situations when interpersonal action coordination performance is best when two agents are both very attentive, predictive and reactive as supposed to situations when for example coordination performance is best if one agent is more predictive, while the other is more reactive? Understanding more about the interplay between the three mechanisms central to social interaction is not only relevant to the study of interpersonal action coordination, but potentially also to the study of inter-brain synchronized patterns. Potentially, asymmetries in inter-brain synchronization observed during social interaction may reflect asymmetries in the extend to which two individuals' actions display attentive, predictive and reactive qualities.

The literature on joint action gives ample evidence for the mechanisms necessary to predict others actions and integrate these predictions into one's own action plans (for review see Knoblich, Butterfill, & Sebanz, 2011; Sebanz et al., 2006; Vesper et al., 2010). Focus has been put on the concept of joint forward models as a core concept of interpersonal action coordination (Hari & Kujala, 2009; Sänger et al., 2011; Vesper et al., 2010) while others have argued that these models are not truly *joint* in that we only have two individual brains and not one joint brain (Gallotti & Frith, 2013). It has been repeatedly shown that during joint action we incorporate the actions of our co-actors into the forward model of our own actions (Freundlieb, Kovacs, & Sebanz, 2015; Sebanz, Knoblich, & Prinz, 2003). Sänger, Lindenberger and Müller have proposed inter-brain synchronized patterns as the neural mechanisms underlying such joint forward models (Sänger et al., 2011). The results of Study II suggest that inter-brain synchronization does not discriminate between two individuals reciprocally updating their forward models or independently of one another holing the same forward models. Therefore, inter-brain synchronized patterns indeed appear to reflect similarities of multiple individuals' action plans. However, I suggest that inter-brain synchronized patterns primarily reflect commonalities in multiple individuals forward models, regardless if these commonalties are due to joint action or not. This is in line with findings "that representing others' tasks is pervasive, occurring outside of joint action" (Vesper et al., 2010, p.1000). Usually however, the forward models of two agents overlap most when these agents are in interaction with one another and attend, predict and react to the same shared stimuli. The situation when two agents momentarily model the world the same way may thus gives rise to the feeling of jointness (Hari, Himberg, Nummenmaa, Hamalainen, & Parkkonen, 2013) – the illusion that another reacts to our inner world. Along these lines, increases in inter-brain synchronization during cooperation as compared to competition could be interpreted as reflecting more overlap in individual forward models in the case of cooperation than competition. For example in the paradigm used by Cui and colleagues (Cui et al., 2012), competition necessitates only attentive and reactive mechanisms, while cooperation

additionally demands predictive mechanisms. This leads to overall more commonalities in individual action plans during cooperation. Menoret and colleagues reported increased beta activity suppression when participants expected a complementary action as compared to when they acted alone, while movement trajectories did not differ (Menoret et al., 2014); another result in line with the interpretation that neural synchronized patterns reflect attentive, predictive and reactive qualities of actions and corresponding commonalities in multiple individuals' forward models.

To conclude, in this dissertation I provided a definition of social interaction that may serve as a starting point to disentangle the impact of individual cognitive mechanisms on inter-brain synchronized patterns. I suggest that inter-brain synchronized patterns do not reflect jointness of actions per se, but rather commonalities in individual action plans that often result from shared stimuli and tasks. Consequently, inter-brain neural synchronized patterns should be most pronounced whenever multiple individuals attend, predict and react to the same stimuli, thus either when they carry out the same task simultaneously in the same environment or when they are in interaction with one another. Future research should address how this, sometimes coincidental, overlap of individual action plans is related to the feeling of jointness. Stanley and Adolphs (2013) called social interaction "an unusually rich and interesting topic, exactly what social psychologists would wish to study and many neurobiologists think is too fuzzy to stud". (Stanley & Adolphs, 2013, p. 5). Given the growing literature on hyperscanning, social neuroscientists apparently already have moved closer to the social psychologist's take on this topic. I close with the hopeful comment that social interaction, when studied using the hyperscanning technique as the actions of multiple agents that involve attentive, predictive and reactive qualities, may continuously become less fuzzy in the eyes of neurobiologists and neuroscientists at large.

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# Teams on the same wavelength perform better: Inter-brain phase synchronization constitutes a neural substrate for social facilitation

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ABSTRACT

Working together feels easier with some people than with others. We asked participants to perform a visual search task either alone or with a partner while simultaneously measuring each participant's EEG. Local phase synchronization and inter-brain phase synchronization were generally higher when subjects jointly attended to a visual search task than when they attended to the same task individually. Some participants searched the visual display more efficiently and made faster decisions when working as a team, whereas other dyads did not benefit from working together. These inter-team differences in behavioral performance gain in the visual search task were reliably associated with inter-team differences in local and inter-brain phase synchronization. Our results suggest that phase synchronization constitutes a neural correlate of social facilitation, and may help to explain why some teams perform better than others.

## Introduction

Teamwork is a prominent feature of today's western working cultures in fields as diverse as science, healthcare, or business (Hall and Weaver, 2001; Hoegl and Gemuenden, 2001; Wuchty et al., 2007). In economics and organizational psychology much research has sought to capture the characteristics of good teamwork, to measure teamwork quality and to identify beneficial aspects of team composition (Ancona and Caldwell, 1992; Bell, 2007; Keller, 2001). Most of the empirical work in these fields did not consider neural mechanisms that facilitate teamwork, but has relied instead on interview protocols and measures of work quality. Delineating the neural mechanisms relevant for teamwork would advance our mechanistic understanding of team dynamics, including the question why working together feels easier with some people than with others.

Social neuroscience, in turn, has often focused on single individuals in 'passive' social contexts, such as observing pictures of social encounters, and has paid relatively little attention to the study of teams or groups. In recent years, however, 'hyperscanning' techniques (Montague et al., 2002), which refer to the simultaneous assessment of the brain activity of more than one person, have helped neuroscientists to study the inter-personal dynamics of neural processes. Experiments using this technique have given rise to a body of research examining the neural processes observed in socially interacting individuals (Babiloni et al., 2007; Dumas et al., 2010; Lindenberger et al., 2009; Sänger et al., 2012, 2013). This move from 'one-body' neuroscience to 'two-body neuroscience' (Dumas et al., 2010) or 'second-person neuroscience' (Schilbach et al., 2013) was informed by theoretical concepts that emphasize the interactive nature of human cognition (Varela et al., 1992). According to these concepts, brain functions cannot be fully understood by observing neuronal subsystems or individuals in isolation; instead, the dynamic interactions among brain, behavior, and environment (Kelso, 1994; Thompson and Varela, 2001) need to be taken into account. In line with this assertion, studies of interacting individuals (Freundlieb et al., 2015; Lachat et al., 2012; Sebanz et al., 2006; Sebanz et al., 2003) have identified cognitive processes that would have gone unnoticed if individuals had been studied in isolation only. For example, Freundlieb et al. (2015)

*Abbreviations*: IPC, inter-brain phase coherence; mc-PLS, mean centered partial least squares; nr-PLS, non rotated partial least squares; *PLI*, phase locking index

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examined when participants adopted another's visuospatial perspective. Only if the other was perceived as an intentionally acting agent, participants consistently adopted their visuospatial perspective.

In addition to representing the partner's intention, neural mechanisms are likely to serve as a substrate for coordinated perception, action, or both. Hyperscanning studies have observed enhanced synchronization of neural processes in interactive paradigms, such as gesturing, finger tapping, guitar play, card play, or speech (for review, see Sänger et al. (2011)). It has been suggested that neural synchronization during joint action may go beyond similarities in perceptual input and motor output and also reflect the synchronization of cognitive processes. To substantiate this point, researchers have tried to extract 'functional relevance' from patterns of neural synchronization. For example synchronization between signal time courses across brains was observed to correlate with story comprehension in speaker-listener settings (Stephens et al., 2010). Similarly, neural synchronization across brains has been reported to reflect leader/follower roles of the participants (Jiang et al., 2015). Cui et al. (2012) reported increased interpersonal coherence in superior frontal cortex during cooperation but not during competition using near-infrared spectroscopy. Sänger et al. (2012) and Konvalinka et al. (2014) were able to distinguish leader/follower roles based on stronger phase locking and stronger frontal alpha suppression in leaders. These initial results fuel the hypothesis that inter-personal as well as intra-personal neural dynamics capture functional characteristics of social interaction.

So far, the majority of studies in the field of hyperscanning research ha focused on joint action. The settings explored range from highly restricted tasks such as finger tapping (Konvalinka et al., 2014) to ecologically valid tasks such as guitar duet play (Lindenberger et al., 2009; Müller et al., 2013; Sänger et al., 2012, 2013) or conversation (Jiang et al., 2015). A major critique to many of the hyperscanning studies mentioned has been the lack of a proper control condition, namely, a condition that is missing the social interactive aspect but keeps most aspects of perceptual input and motor output constant relative to the social condition. Here, we propose a paradigm that includes such a control condition by investigating an essential aspect of joint action that does not involve motor output: joint attention. Joint attention has been found to play a crucial role in social interaction (Tomasello, 1995) and particularly joint action (Sebanz et al., 2006). Joint attention entails that "two individuals know that they are attending to something in common" (Tomasello, 1995, p.106), and can be seen as providing "a basic mechanism for sharing representations of objects and events" (Sebanz et al., 2006, p.70). Hence, it constitutes a core feature of joint action, and of teamwork in general.

Joint action typically requires joint attention, but the inverse is not necessarily true, that is, there can be joint attention without joint action, such as when people are jointly looking at a photo. Also, the very same object (e.g., photo) can also be attended to alone. Thus, comparing joint attention to individual attention makes possible what hyperscanning studies have generally failed to achieve, namely, to compare two conditions, in the absence of synchronized motor activity, that vary on the social dimension without varying the perceptual setup.

The aim of the present study was to assess whether synchronization in inter-brain dynamics reflects a modulation of cognitive processes by social facilitation or merely the presence of a common driver, such as shared perceptual input. Social facilitation subsumes changes in behavioral performance associated with the passive or active presence of another person (Allport, 1920; Zajonc, 1965). For this purpose, we chose to investigate differences between individual and joint attention. We embedded individual and joint attention in a visual search task, which was carried out either individually or in dyadic teams. This setup enabled us to first analyze differences in neural dynamics between individual and joint attention and to then relate these neural differences to behavioral performance differences between individual work and teamwork. This teamwork went beyond the period of initial joint attention studied in the first step and includes the coordination of a joint response. The current study thus explores joint attention as an important aspect of teamwork in two ways: first by analyzing intra- and inter-brain neural dynamics of joint attention and second by relating them to behavioral team performance proficiency (see Fig. 2).

To investigate the performance benefits of joint attention, we used an adaptation of Miller's Race Model Inequality (RMI; (Miller, 1982; Ulrich et al., 2007)) to separate the collaborative benefit of teamwork from the benefit that would be expected under the assumption of processing independence. Miller's RMI was originally developed to test whether two target signals were processed in one mind as a race between independent activations (with the faster signal determining the response on each occasion) or whether the signals were co-activated (signal activations were combined prior to the response decision). We apply the same logic and method here, testing whether responses by two-person teams reflect a race between independently processing individuals (with the faster person eliciting the valid response) or whether teams collaborated prior to the response (i.e., shared the task and exchanged information).

It should be kept in mind that team performance has both benefits and costs. On the one hand, cognition can be made more efficient when collaborators divide the cognitive load of the task (Houtkamp and Roelfsema, 2009). On the other hand, coordinating joint performance through speech or gesture requires effort and time (Brennan et al., 2008). Our measure of team performance captures some mix of these benefits and costs and reflects the overall collaborative benefit/cost for each team. If inter-brain dynamics indeed reflect the synchronization of cognitive processes, they should vary with the degree (and potentially the benefit) of social interaction, and might correlate (positively) with behavioral team performance. Thus, the present study was guided by two specific hypotheses: (a) Inter-brain synchronization will be greater in a social context than in a comparable setting that does not engage joint attention; (b) between-pair differences in inter-brain neural dynamics will correlate with between-pair differences in task performance.

## Material and methods

### *Participants and data analysis*

#### *Research participants*

Fifty-two healthy individuals participated in the study, forming a total of 26 non-overlapping pairs, 13 male-male pairs and 13 female-female pairs. The age of the participants ranged from 18 to 30 years (mean age = 25.2, SD = 3.43). One male pair had to be excluded from the analysis due to a technical problem, thus 25 pairs (13 female, 12 male) were retained in the EEG data analysis. Four pairs (three female, one male) had to be excluded from behavioral data analysis due to technical problems with data recording. Thus 21 pairs (10 female, 11 male) were included in the behavioral analyses, and the brain-behavior regression analyses. Participants were randomly assigned to pairs and did not know each other prior to the experimental session. At the beginning of each experimental session, participants filled out questionnaires that assessed personality (NEO Five-Factor-Inventory, Costa and McCrae, 1992) and interpersonal values (Circumplex scales of interpersonal values, Locke, 2000). While being prepared for the EEG session the two participants were placed in front of each other and asked to talk to get to know one other. All pairs talked about study subjects and hobbies/interests for ca. 10 min, after which the experimenter asked them to stop talking and to enter the EEG cabin. All pairs took part in another EEG-experiment before starting the visual search task. All participants volunteered for the experiment, and gave their written informed consent prior to their inclusion in the study. The Ethics Committee of the Max Planck Institute for Human Development approved the study. The study was performed in accordance with the ethical standards laid down in the 1964 Declaration of Helsinki.

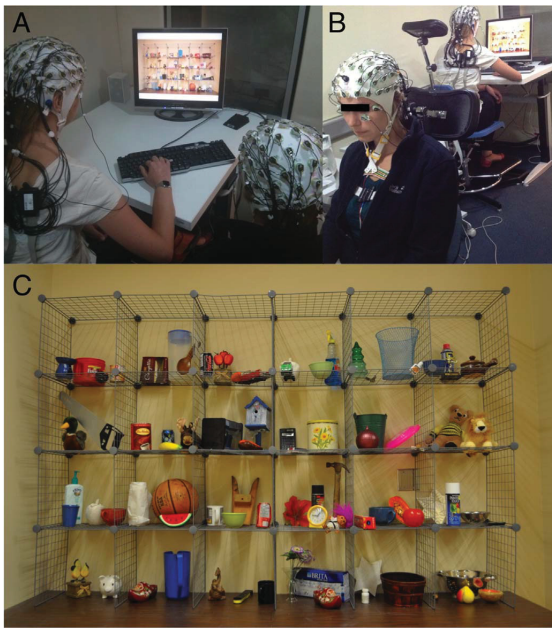


**Fig. 1.** Experimental set-up in the electromagnetically shielded cabin. A. EEG measurement of one participant in the individual condition. B. Two participants being measures in the social condition. C. Example of a search display.

*Behavioral method: enumeration visual search task*

Experimental displays depicted shelves containing objects commonly found in a home or office (see Fig. 1 for an example display). Each display contained 82 distractor objects in one of four different configurations, and zero, one, or two of four possible target objects. The same target never appeared twice in the same display and each appeared equally often in each quadrant. This generated 356 displays: four without a target, 64 with one target, and 288 with two targets. Experimental sessions consisted of a total of 42 trials: 14 trials each with zero, one, and two targets. Search displays for each session were selected using weighted random sampling of the 356 total search displays. Displays subtended 37°×30° visual angle on a 19-inch computer monitor (screen resolution 1280×1024 pixels). Matlab 2010a software and Psychtoolbox3 were used to control the experiment.

During the experiment participants indicated as rapidly and accurately as possible the number of targets present in a display by pressing keys labeled '0', '1', and '2'. Participants completed two experimental sessions: one individually (individual condition) and one as a team with another participant (social condition). Session order was randomly counterbalanced across pairs (individual first, social first). When completing the task individually, participants sat in front of their respective computers and entered responses on their respective keyboard. When completing the task as a team, participants sat side by side in front of a shared computer and entered one joint response using a shared keyboard. One participant replied during the first half of the experiment, the other participant during the second half. Teams were instructed to use whatever strategy they thought was best for working together and individuals were instructed to use whatever strategy they thought was best. Participants received feedback about their percentage of correct responses every 7 trials. Teams were allowed to interact as they wished (talking, gesturing, touching, etc.). Both teams and individuals were instructed to avoid unnecessary movements to prevent EEG artifacts. Measurements took place in an electromagnetically shielded cabin.

*EEG data acquisition*

The EEG was recorded with active 64 Ag/AgCl electrodes per person, placed according to the international 10–10 system, with the reference electrode at the right mastoid (actiCAP, Brain Products, Munich, Germany). Separate amplifiers (BrainAmp DC, BrainProducts, Munich, Germany) with separate grounds were used for each individual, linked to one computer. Vertical and horizontal electrooculograms (EOGs) were recorded to control for eye blinks and eye movements. All channels were recorded at a sampling rate of 5000 Hz. A 0.016–1000 Hz bandpass filter was used. Triggers were sent from the stimulus presentation computer to the EEG-recording system for stimulus onset. One stimulus computer with three synchronized screens was used for stimulus presentation. Two screens were placed inside the cabin whereas one control display was placed outside the EEG cabin to monitor stimulus presentation.

*Behavioral data analysis*

Following Brennan and Enns (2014), correct RT and accuracies were first subjected to a repeated measures analysis of variance (ANOVA) examining the factors of condition (team, average individual) and session order (individual first, social first). In a second step, the algorithm and MATLAB routines provided in Ulrich et al. (2007) were adapted to compare team performance to the expected performance of the two individuals under the independence assumption (Brennan, 2014; Brennan and Enns, 2014).

Team efficiency was calculated in three steps. First, cumulative density functions (CDFs) of each team's correct RTs were generated ($CDF_{team}$). Each CDF contained a total of 42 correct RTs, minus the errors committed. Second, CDFs of the optimal performance of two individuals under an assumption of independence were generated by combining the two individual team members' correct RTs into one distribution ($CDF_{optimal\ individual}$), and then truncating this distribution at the number of RTs in $CDF_{team}$. Third, a team efficiency value was generated for each team by subtracting $CDF_{team}$ from $CDF_{optimal\ individual}$. This method approximates the statistically expected distribution of team responses if the two individuals worked independently by assuming that the faster of the two would respond in each trial, and compares it to the actual team distribution. The difference between the two distributions provides an index of team benefit.

*EEG data analysis*

*Preprocessing*

EEG data were filtered with a high-pass filter at 0.5 Hz and resampled at 1000 Hz. Thereafter, they were subjected to semi-automatic independent component analysis (Vigário, 1997) as implemented in Brain Vision Analyzer 2 as Ocular Correction ICA (Brain Products). This algorithm is optimized to detect and highlight components that likely reflect eye movements to minimize possible confusion with components reflecting, e.g., delta activity. Mean slope algorithm was used for blink detection. By using a fast ICA extended algorithm for ICA decomposition, one component was extracted per EEG channel. All EEG electrode channels were included (minus reference and eye electrode channels) yielding a total of 60 components. We visually inspected topographies and time courses of all components and rejected components that reflected blinks, horizontal eye movements, ECG, muscle activity and line noise. Across subjects on average twelve out of the 60 components were rejected. Spontaneous EEG activity was then segmented into epochs of 1200 ms (200 ms before stimulus onset until 1000 ms after stimulus onset), and we removed all epochs containing remaining artifacts from head or body movements by visual inspection. In the alone condition, on average 38 out of 45 trials (SD = 4.58) were included in the analysis as artifact-free segments; in the social condition, on average 38 trials (SD = 4.11) were included. It is important to note that the EEG data analyzed was recorded during an

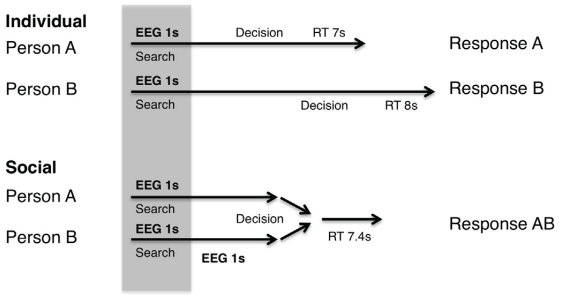


**Fig. 2.** Conceptualization of EEG analysis in relation to behavior. The hypothesized decision-making processes during one enumeration visual search trial in the individual and social condition is shown. Analyzed EEG epochs are highlighted in grey.

interval where no movement or decision-making was involved: only the first second after stimulus onset was analyzed out of an average trial duration of 7.4 s (see Fig. 2).

*Synchronization measures*

Segments were analyzed using a complex Morlet wavelet (c = 5) that transformed the EEG time series into a complex time-frequency signal for frequencies from 2 to 20 Hz, in steps of 2 Hz (10 frequency values in total). Two synchronization measures, *PLI* and *IPC*, were obtained from the corresponding time-frequency matrices (Müller et al., 2009). The phase locking index (*PLI*) reflects the invariance of phases at a single electrode across $N$ trials in the time-frequency domain and is defined by

$$PLI_k(t,f) = \left| \frac{1}{N} \sum_n^N e^{j\varphi_k^n(t,f)} \right|, \quad j = \sqrt{-1}$$

where $\varphi_k^n(t,f)$ is the phase of the $n$th trial at time $t$ and frequency $f$ of a specific electrode $k$. The intra- and inter-brain phase coherence represents the degree of constancy in phase difference across $N$ trials between two electrodes measured from one or two brains simultaneously. It is defined in a similar way as

$$IPC_{kl}(t,f) = \left| \frac{1}{N} \sum_n^N e^{j\Delta\varphi_{kl}^n(t,f)} \right|, \quad j = \sqrt{-1}$$

with the phase difference between electrodes $k$ and $l$ at trial $n$, time $t$ and frequency $f$, being equal to:

$$\Delta\varphi_{kl}^n(t,f) = mod(\varphi_k^n(t,f) - \varphi_l^n(t,f), 2\pi)$$

The phase difference is calculated between two electrodes of the same brain for intra-brain phase coherence or between two electrodes of two different brains for inter-brain phase coherence (IPC). We selected 21 electrodes per person (Fp1, Fpz, Fp2, F7, F3, Fz, F4, F8, T7, C3, Cz, C4, T8, P7, P3, Pz, P4, P8, O1, Oz, and O2) and included all possible pairs of these electrodes in this analysis. This selection reduces a possible bias in functional connectivity findings produced by volume conduction, while still covering the entire cortex (cf. Lindenberger et al., 2009; Sänger et al., 2012). We calculated PLI and intra-brain phase coherence per participant and *IPC* per pair.

*PLI* and intra-brain phase coherence capture phase locking within one individual brain, while *IPC* captures phase locking between two brains. All measures were calculated across all trials that were included in the analysis (mean 38 trials) and for each millisecond of the 1200 ms segment length.

*Statistical evaluation of synchronization measures*

Partial Least Squares is a multivariate statistical method that is suitable for revealing the relationship between two blocks of datasets, and has been used extensively in the neuroimaging literature (Abdi, 2010; McIntosh et al., 1996; McIntosh and Lobaugh, 2004). Here, it was used to examine associations between synchronization measures, on the one hand, and the vectors coding for the experimental design, on the other hand. The method is based on a decomposition of the covariance of the two blocks in a set of new variables that optimally relate them, with optimality referring to explaining as much of covariance with as few dimensions as possible.

In this study, we used two versions of the method: non-rotated contrast PLS ("nr-PLS") to test the specific hypotheses that differences in brain data co-vary with differences in condition or session order and mean centering task PLS ("mc-PLS") to explore the data for additional effects, e.g., for a possible interaction between condition and session order. As we had no strong a priori hypothesis for the exact 'shape' of a potential interaction between condition and session order, we made use of the mc-PLS data-driven approach.

Both PLS versions start by constructing a brain data matrix for each experimental group. Rows in this data matrix correspond to participants within condition and, thus, in our case, to participant pairs. Consequently the data matrix is made up of NPairs×NCondition rows. Columns in the data matrix correspond to all data points or elements (i.e., in our case, *PLI* values per electrode or *IPC* values for each pair of electrodes, across all frequencies and time points in either case). Then, participants' rows are averaged column-wise within conditions, and the data matrices of all groups are concatenated into a single matrix, **M**, with rows corresponding to conditions within groups (NConditions×NGroups, in total), and data elements for columns. At this point, in the case of the mcPLS, the grand average is removed by all conditions' rows column-wise, and the modified matrix **M** undergoes a singular value decomposition **U*****S*****V** = SVD(**M**), which yields three matrices: (i) the orthonormal matrix **V** of the *saliences of the contrasts* (i.e., the *task design latent variables* describing the relations among the conditions and groups of our design for each contrast); (ii) the orthonormal matrix **U** of *element saliences* that are proportional to the covariance of each data element with each one of the task contrasts (i.e., the *brain latent variables*); and (iii) the diagonal matrix **S** of *singular values* that are proportional to the variance explained by each contrast. The number of resulting singular values, one for each contrast, depends on the degrees of freedom of the design, being, in our case, NConditions×NGroups −1 = 3. Furthermore, the multiplication **B** = **M*****U** produces a matrix of *brain scores* that indicate the strength of the task effect of each contrast per participant pair and condition. In other words, the brain score of a particular participant pair for a specific contrast and condition is the covariation of the brain data of this participant pair for that condition with the corresponding brain latent variable vector of the contrast in question.

As for the nr-PLS, instead of undergoing a SVD, it requires an orthonormal matrix **C** of predefined contrasts to be tested as a priori hypotheses. Then, **U** = $(\mathbf{C}^{T}*\mathbf{M})^{T}$, where $(.)^{T}$ is the operator of matrix transposition, **V** = **C**, and $s_i = \sqrt{\sum_j u_{ji}^2}$, where $s_i$ are the elements of the diagonal of **S** (one for each contrast) and $u_{ji}$are the elements of **U**. In our case, we tested the main effects of conditions and session order, i.e, contrasts [1 −1 1 −1] and [1 1 −1 −1] before normalization, respectively.

PLS addresses the problem of multiple comparisons for statistical significance via a permutation test and the problem of element-wise reliability via a bootstrap resampling test. The permutation test is performed on the singular values with resampling of the initial data matrices across conditions and groups without replacement. This permutation test yields a p-value for each task latent variable, i.e., for each contrast. For the bootstrap test, the initial data matrix is resampled with replacement within conditions and groups. For the task latent variables we plotted intervals of 95% confidence. For the brain latent variables, we calculated bootstrap ratios by dividing each element with its standard error as calculated by the corresponding bootstrap sample distribution. Bootstrap ratios greater than 2.5758

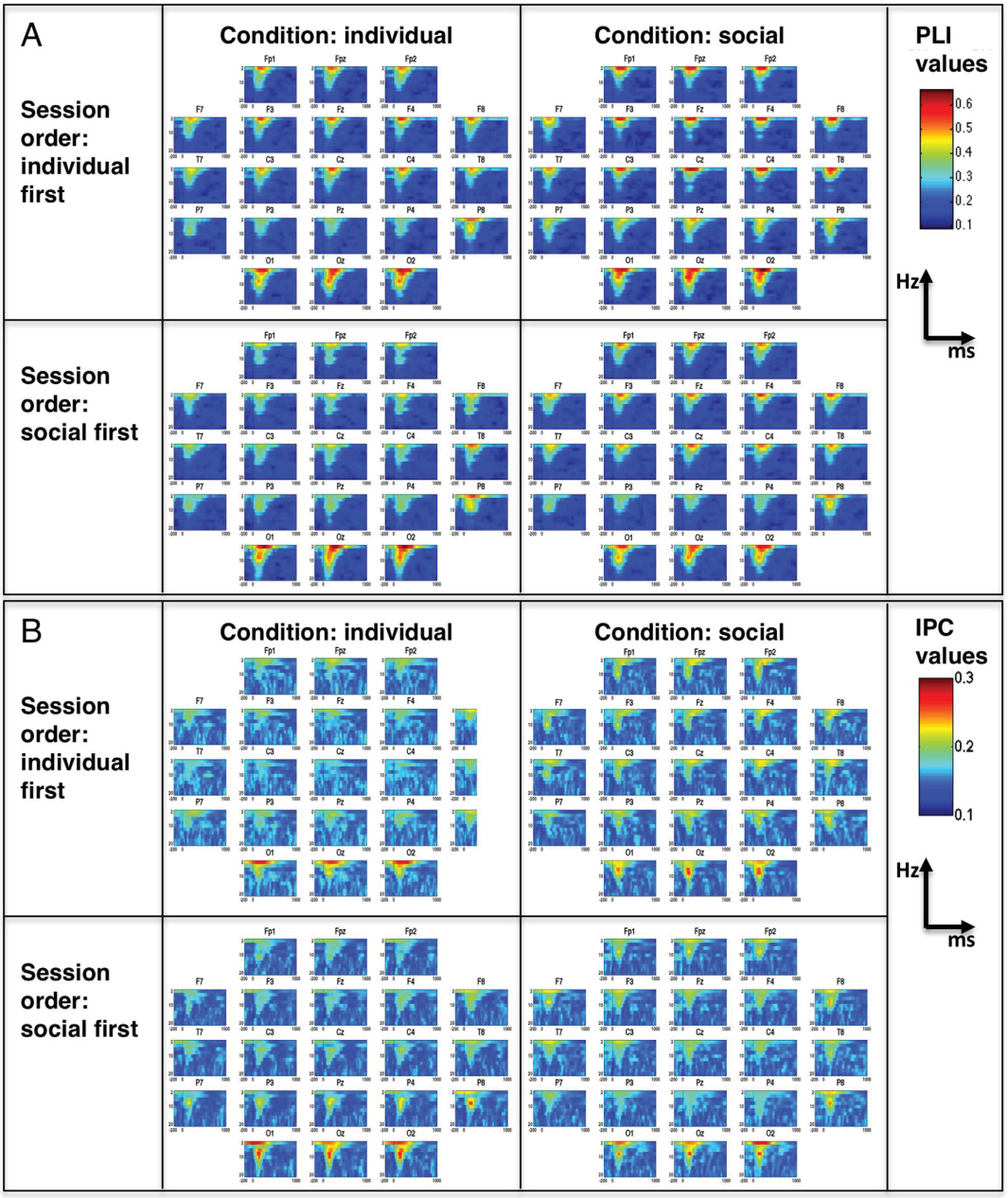


**Fig. 3.** Grand average *PLI* and *IPC* results, grouped by condition and session order. A. *PLI* values were averaged across all subjects at each of the 21 electrode sites for each frequency band (2, 4, 6, 8, 10, 12, 14, 16, 18, and 20 Hz). Electrode sites are indicated above each subplot. The colormap is anchored at the lowest and highest values. B. *IPC* values from one electrode site in subject A to all other electrode sites in subject B were averaged for each frequency band (2, 4, 6, 8, 10, 12, 14, 16, 18, and 20 Hz). This averaging procedure was repeated for all 21 electrode sites of subject A. Values were then averaged across all pairs. Electrode sites are indicated above each subplot. The colormap is anchored at the lowest and highest values.

approximate the 99th two-tailed percentile for a particular element (see Z-score table). In the connectivity plots we only plotted connections that exceeded this value. We constructed connectivity plots in Matlab, using the BrainNet Viewer software (Xia et al., 2013).

*Correlations between neural and behavioral measures*

PLS analyses create a latent variable similar to a factor. This latent variable represents the pattern of neural synchronization that best distinguishes the behavioral conditions across all individuals. A ‚brain

score', similar to a factor score, can be computed for each pair for each condition that reflects how strongly that pair expresses the corresponding neural pattern. We computed brain scores for each pair using the latent variables identified by the PLS analyses. We then entered these brain scores into a series of three regression analyses and tested them hierarchically with model comparisons to evaluate how well brain phase synchronization predicted behavioral team performance. We also calculated mean and difference scores within dyads for the NEO-Five-Factor-Inventory (for all five domains) and for the Circumplex scales of interpersonal values (for CSIV mean) to assess correlations between personality measures, neural measures, and team efficiency.

## Results

### *Behavioral results*

#### *Correct response time (RT) and accuracy*

Teams generally responded faster (mean difference = 1.72 s, $F(1,194) = 7.43$, $p < 0.01$) and less accurately (mean difference = 17%, $F(1,194) = 42.73$, $p < 0.01$) than average individuals tested alone. These analyses also indicated that the condition tested first was slower in *RT* (mean difference = 2.08 s, $F(1,194) = 27.94$, $p < 0.01$) and more accurate (mean difference = 12%, $F(1,194) = 16.74$, $p < 0.01$) than the same condition tested second. Finally, social dimension interacted with session order in *RT*, such that when the social condition was tested second it resulted in larger gains in *RT* (mean difference = 5.30 s, $F(1,194) = 19.95$, $p < 0.01$) than when the individual condition was tested second (mean difference = 0.45 s). Search accuracy did not interact in this way ($F(1,194) < 1.0$).

#### *Team efficiency*

Based on RMI, we calculated and compared *RT* cumulative density functions for team and individuals to control for the statistical advantage of sampling from two instead of one response distribution. Specifically, we compared the optimal individual cumulative density function with the team cumulative density function using multiple Bonferroni-corrected paired sample t-tests at four percentiles. This analysis showed that two-person team performance was not reliably faster than optimal individual performance, ($t(21) = 0.56, 0.38, 0.84, 3.70, -2.01$, at percentiles 0.20, 0.40, 0.60, and 0.80, respectively, all $p > 0.65$). Though team performance, on average, did not surpass expectations based on individual performance, team efficiency (values are still appropriate to compare individual and team performance, and to compare different teams with one another. Importantly, team efficiency scores varied between teams (min = −8466 ms, max = 6012 ms), indicating that the benefits and collaboration outweighed the costs for some teams, while for others the costs outweighed the benefits.

### *EEG results*

Given that we observed an interaction between social dimension and session order in the behavioral data, we approached the EEG data analysis along the same lines: separating the analysis in terms of social dimension (individual/social) as well as session order (individual condition first/ social condition first).

#### *Phase-locking index*

Grand average across pairs showed generally higher phase locking in the social condition, especially at low frequencies and frontal sites (see Fig. 3).

Fig. 4 shows PLS-based statistical significance plots. Mc-PLS contrasting *PLI* in both conditions grouped by session order did not reveal any significant differences between groups or conditions ($p > 0.1$ for all latent variables). Testing with Nr-PLS, specifically the hypothesis that differences in condition or session order co-varied

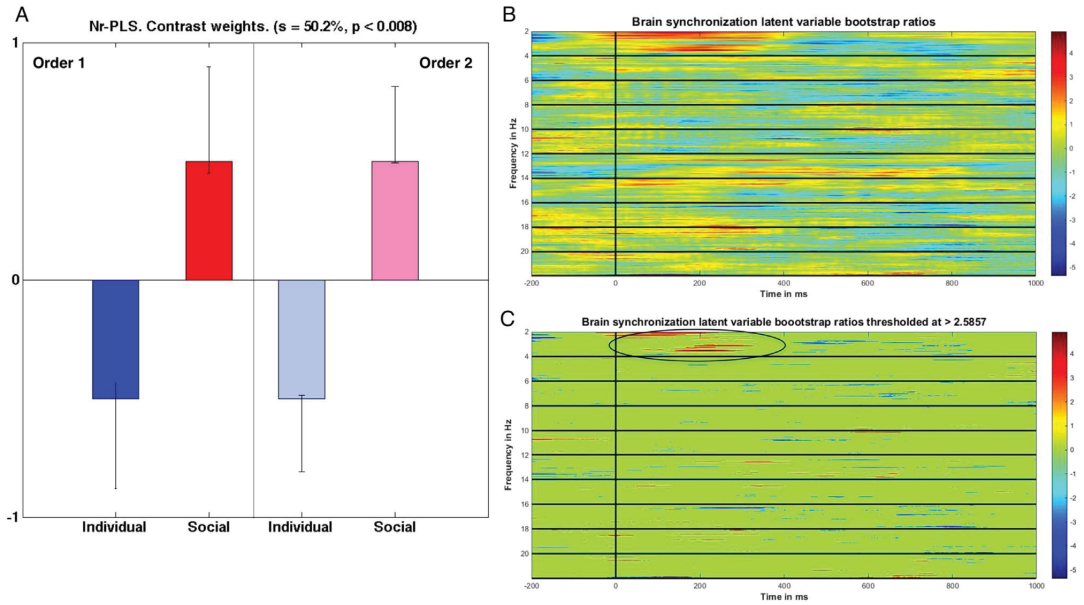


**Fig. 4.** Nr-PLS on *PLI* revealed higher *PLI* values in the social condition. A. Mean of subjects' brain scores per condition, mean-centered and normalized with the corresponding singular value (s), and 95% confidence intervals (CI) derived from the bootstrap test. Order 1 = session order with the individual condition first. Order 2 = session order with the social condition first. B. Brain synchronization latent variable bootstrap ratios before thresholding. Each horizontal line corresponds to one electrode at the indicated frequency (42 channels per frequency, grouped from frontal to occipital within frequencies). The colormap is anchored at the lowest and highest values. X-axis: time in ms; Y-axis: channels grouped by frequency (black lines indicate frequency boundaries) C. Analogue to (B) with brain synchronization latent variable bootstrap ratios thresholded at bootstrap ratios > 2.5857 (99% CI). Strongest effects are indicated by black ellipses.

with *PLI*, showed no significant effect for session order either ($p = 0.92$), but a significant main effect for condition ($p < 0.01$). A strong increase of synchronization during the social condition was especially observed for the 2 Hz frequency bin.

*Intra- and inter-brain phase coherence*

Grand average across all pairs and all electrodes showed a difference in *IPC* similar to the pattern observed for *PLI* (Fig. 3). Generally, *IPC* was increased in the social condition relative to the individual condition. As with *PLI*, we assessed *IPC* with two PLS analyses. A nr-PLS contrasting conditions and grouping by session order showed no effect for session order ($p = 0.53$), but a significant main effect for social condition ($p < 0.01$, see Fig. 5). With Mc-PLS we found a contrast that showed a difference between conditions, modulated by session order (see Fig. 5). The first latent variable depicting this interaction explained 35.5% of the variance of *IPC* at a significance level of $p < 0.005$. The other latent variables did not show any significant effects ($p > 0.1$ for all latent variables). The patterns of brain latent variables' bootstrap ratios for both PLS analyses were highly similar to each other (see Fig. 5), suggesting that social condition was indeed a major modulator of *IPC*. Consequently, we focused on the Nr-PLS results in the next steps as they reflected explicitly the effect of social condition. Unlike for *PLI*, modulation of *IPC* was not clearly stronger in one frequency bin than in others. However, similar to the *PLI* results, sustained increases of synchronization were particularly observed in the 2 Hz frequency bin at 200–600 ms post stimulus onset. Increases of *IPC* were followed by a particularly pronounced decrease of synchronization at 8 Hz 300–400 ms post stimulus presentation (see Fig. 5). Generally, initial increases of *IPC* were followed by later decreases across frequency bins.

To control for general changes in connectivity within one brain that could drive the differential *IPC* results during the social condition, we calculated intra-brain phase coherence. Neither mc-PLS ($p > 0.05$ for all latent variables), nor nr-PLS ($p > 0.1$ for all latent variables) detected any significant covariance between intra-brain phase coherence and condition or session order.

*Connectivity plots*

PLS results revealed a main effect for condition on both *PLI* and *IPC* that for *IPC* was also modulated by the presence of session order.

PLS results revealed a main effect for condition on both *PLI* and *IPC*, which for *IPC* was also modulated by session order. In a next step, we sought to better visualize which electrodes/connections showed the most pronounced modulation by social condition and to assess whether the electrodes that showed strong modulation of *PLI* were the same electrodes that showed strong modulation of *IPC*. We thus constructed connectivity plots on the nr-PLS results for the 2 Hz frequency bin (see Fig. 6A), as the previous analysis steps had revealed strong synchronization increases at 2 Hz for both *PLI* and *IPC* (compare Figs. 4 and 5). We additionally constructed connectivity plots for the 8 Hz frequency bin (see Fig. 6B), as in this frequency bin strongest synchronization decreases appeared (compare Fig. 5). We constructed connectivity plots based on the first latent variable identified in the nr-PLS as this contrast captured explicitly the effect of condition not modulated by session order.

*Associations of intra- and inter-individual brain measures to behavioral team efficiency*

Finally, we examined linear associations between changes in neural phase synchronization and changes in behavioral team performance. Our behavioral analyses showed that some teams benefited more from working together than others. Is neural phase synchronization enhanced in pairs that make better teams? To test this hypothesis we used team efficiency scores as a proxy for behavioral benefit of working together and brain scores computed by the PLS analyses (see methods section) as a proxy of average local (*PLI*) and inter-brain (*IPC*) phase synchronization during individual and social conditions. Our behavioral analysis had revealed a strong relation between team efficiency scores and session order. To test if local phase synchronization in one player (brain scores *PLI*) and/or inter-brain phase synchronization between players (brain scores *IPC*) explained *additional* variance in team efficiency, we conducted a series of three hierarchical regression analyses and tested whether adding the relevant predictors was associated with a reliable increase in the amount of explained variance.[1]

Model No. 1:

$$y_i = \beta_0 + \beta_1 x_i + \varepsilon_i$$

Model No. 2:

$$y_i = \beta_0 + \beta_1 x_i + \beta_2 v_i + \beta_3 w_i + \varepsilon_i$$

Model No. 3:

$$y_i = \beta_0 + \beta_1 x_i + \beta_2 v_i + \beta_3 w_i + \beta_4 a_i + \beta_5 b_i + \varepsilon_i$$

where **y** denotes team efficiency values, **x** is session order, **v** is nr-PLS brain scores on *PLI* during individual condition, **w** is nr-PLS brain scores on *IPC* during individual condition, **a** is nr-PLS brain scores on *PLI* during social condition, **b** is nr-PLS brain scores on *IPC* during social condition, and $\varepsilon$ is a realization of a random variable with distribution $n(0, \Sigma\varepsilon^2)$.

The first model contained only session order as a predictor for team efficiency scores. As expected, session order explained a significant amount of variance in team efficiency score ($F(18) = 14.29$, $p < 0.005$, $R^2 = .44$, $R^2$ adjusted = .41, session order (social first): −3840, SE = 1016, $t(18) = -3.78$, $p < 0.005$). For the second model, brain scores obtained by nr-PLS on *PLI* and IPC during the individual condition were added as predictors. Brain scores were added as absolute values. Adding these measures of phase synchronization during the individual condition reliably increased the amount of explained variance ($\Delta R^2 = 0.25$, $\Delta R^2$ adjusted = 0.22, $F(2) = 6.443$, $p < 0.01$).The third model additionally contained nr-PLS brain scores on *PLI* and *IPC* during joint attention. Adding measures was again associated with a reliable increase in explained variance ($\Delta R^2 = 0.11$, $\Delta R^2$ adjusted = 0.10, $F(2) = 4.139$, $p < 0.05$). Table 1 reports the regression and partial correlation coefficients for the full model. As can be seen, session order, brain scores obtained by nr-PLS on *IPC* during the individual condition, and brain scores obtained by nr-PLS on *PLI* during.

the social condition uniquely predicted team efficiency score. We observed the same pattern of results when using mc-PLS brain scores instead of nr-PLS brain scores.

We also computed partial correlations between behavioral changes (team efficiency scores) and changes in local phase locking/inter-brain synchronization (nr-PLS brain scores on *PLI/IPC* during social minus nr-PLS brain scores on *PLI/IPC* during individual condition) controlling for the effect of session order. Both partial correlations were reliably different from zero (for changes in *PLI*: $r(20) = 0.50$, $p < 0.05$; for changes in *IPC*: $r(20) = 0.58$, $p < 0.01$; see Fig. 7). *PLI* and *IPC* nr-PLS brain scores for the social condition were correlated among themselves ($r(18) = 0.53$, $p < 0.05$), while *PLI* and *IPC* nr-PLS brain scores were not significantly correlated among each other for the individual condition ($r(18) = 0.18$, $p = 0.46$).

To summarize, adding measures of neural phase synchronization as predictors of behavioral change in visual search almost doubled the explanatory power compared to a regression that only included the effect of session order as a predictor ($R^2$ adjusted 0.41 vs. $R^2$ adjusted 0.74, $F(4) = 6.55$, $p < 0.005$). Neural phase synchronization between two players' brains during individual attention predicted their average behavioral benefit from working as a team. Adding measures of phase

[1] The residuals of one dyad exceeded Cook's distance; that dyad was therefore excluded from the regression analyses.

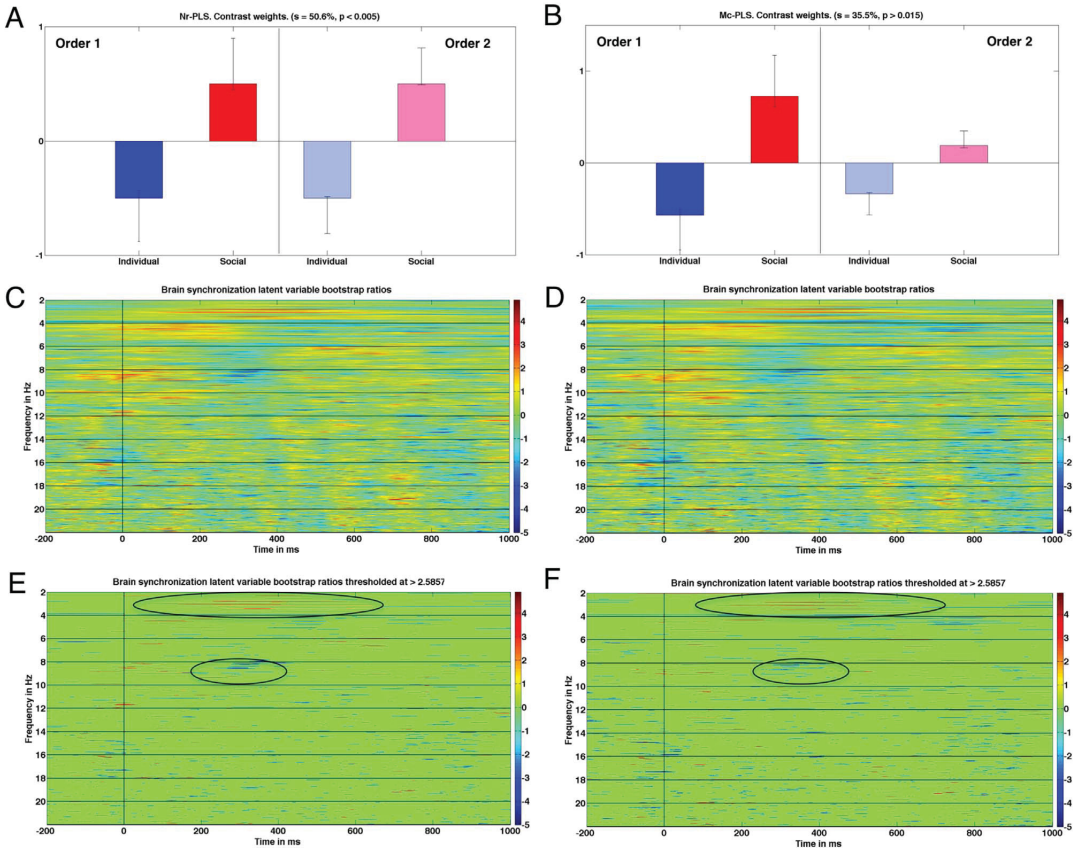


**Fig. 5.** Nr-PLS and Mc-PLS on *IPC* reveal higher *IPC* values in the social condition. PLS was performed twice on *IPC* values. A. Shown are the results obtained by Nr-PLS. Mean of subjects' brain scores per condition, mean-centered and normalized with the corresponding singular value (s), and 95% confidence intervals derived from the bootstrap test. B. Brain synchronization latent variable bootstrap ratios before thresholding, obtained by Mc-PLS. Each horizontal line corresponds to one electrode connection at the indicated frequency (441 connections per frequency, grouped from frontal to occipital within frequencies). The colormap is anchored at the lowest and highest values. x-axis: time in ms. y-axis: channel connections grouped by frequency (black lines indicate frequency boundaries). Panel C (for Nr-PLS results) shows brain synchronization latent variable bootstrap ratios after thresholding at bootstrap ratios > 2.5857 (99% CI). One strong synchronization and one strong desynchronization effect are indicated by black ellipses. D. Values were derived in the same way as in (A), but estimated by Mc-PLS. E. Analogue to (C), but values obtained by Nr-PLS. F. Analogue to (D) but for Mc-PLS results. Strongest effects for Nr-PLS results in (E) are indicated by black ellipses in both (E) and (F).

synchronization during dyadic performance was associated with further increments in prediction of team efficiency. Finally, change-change correlations controlling for session order confirmed that individuals showing more positive changes in *PLI* and *IPC* from individual to dyadic performance also showed more positive changes in visual search performance.

We did not observe any correlation with p-values smaller than 0.05 between personality measures, team efficiency and neural measures.

## Discussion

Many earlier studies in the field of hyperscanning and social interaction have focused on interpersonal action coordination (Dumas et al., 2010; Dumas et al., 2011; Konvalinka et al., 2014; Lindenberger et al., 2009; Müller and Lindenberger, 2014; Müller et al., 2013; Sänger et al., 2012, 2013). Here, we investigated whether inter-brain synchronization can also be observed in a joint-attention setting that requires no coordinated body movements. Specifically, we addressed two main research questions: (i) Do neural processes presumably associated with joint attention manifest themselves in increased inter-brain phase synchronization? (ii) Are between-dyad differences in performance gain from working as a team associated with between-dyad differences in phase synchronization during joint attention?

The results of the present study support positive answers to both questions. PLS analyses on local phase locking within one brain (measured by *PLI*) and phase locking between two brains (measured by *IPC*) revealed significantly higher *PLI* and *IPC* values during joint attention than during individual attention (see Figs. 4 and 5). These results suggest that within- and between-brain dynamics are susceptible to social context, resulting in higher local intra-brain as well as higher inter-brain phase synchronization when social context is made salient.

We chose to study joint attention vs. individual attention during a visual search task to improve control of condition differences in perceptual input and motor output. To address this goal, we presented identical pictures in our two experimental conditions (individual vs. team) and instructed participants to focus on the center of the screen at the beginning of each trial to reduce peripheral view of the partner in the social condition to a minimum. We further restricted the EEG data analysis to brief periods one second after picture onset to avoid potential confounds arising from finger movements. We observed

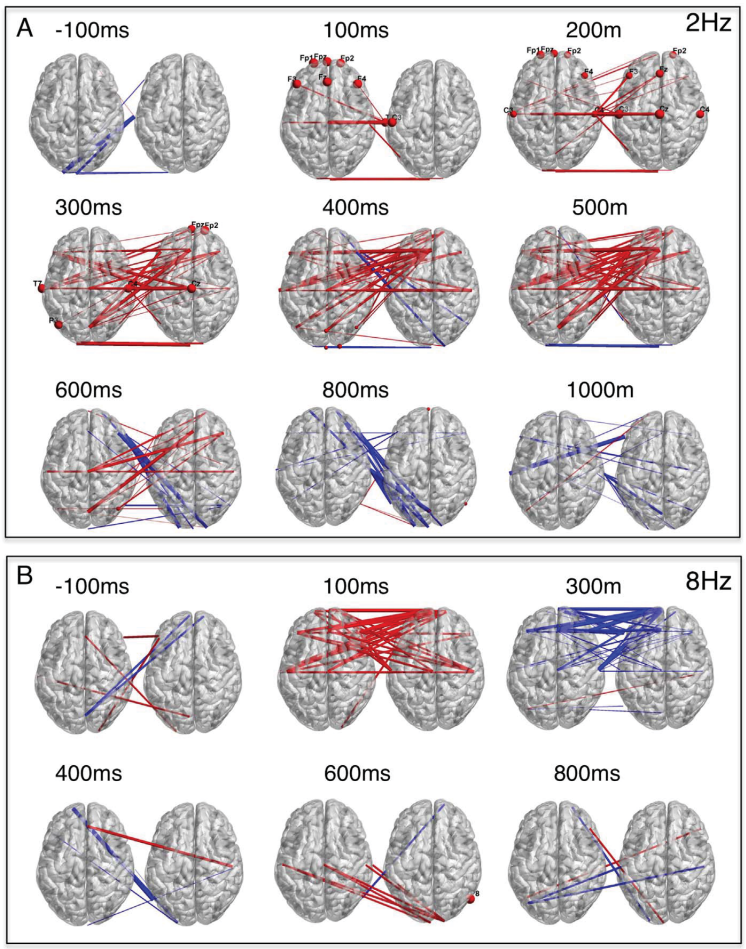


**Fig. 6.** Time course of *PLI* and *IPC* at (A) 2 Hz and (B) 8 Hz. A. *PLI* and *IPC* values per electrode and electrode connection at 2 Hz. B. *PLI* and *IPC* values per electrode and electrode connection at 8 Hz. Nodes = *PLI*. Edges = *IPC*. Values are thresholded at > 2.5758 bootstrap ratios (approximating 99% CI). Significant nodes are labeled with the corresponding electrode name. Blue codes for negative values. Red codes for positive values.

**Table 1**
Regression coefficients and semi-partial correlation coefficients estimated for the multiple linear regression model no. 3. Dependent variable = Team Efficiency Score. *PLI/IPC* individual = brainscores estimated by nr-PLS on *PLI/IPC* during the individual condition. *PLI/IPC* social = brainscores estimated by nr-PLS on *PLI/IPC* during the social condition. *B* = unstandardized regression coefficients. SE = standard error. beta = standardized regression coefficients. sr = semi-partial regression coefficients.

| Variable | *B* | SE *B* | beta | sr | *t*(14) | *p* |
|---|---|---|---|---|---|---|
| **Intercept** | −9856.33 | 2417.49 | 0 | 0 | −4.077 | 0.001 |
| **Session order** | −2191.64 | 747.89 | −0.38 | −0.55 | −2.930 | 0.011 |
| ***PLI* individual** | 14.03 | 66.34 | 0.03 | 0.05 | 0.211 | 0.836 |
| ***IPC* individual** | 364.77 | 107.89 | 0.48 | 0.54 | 3.381 | 0.004 |
| ***PLI* social** | 158.06 | 61.44 | 0.38 | 0.44 | 2.573 | 0.022 |
| ***IPC* social** | −5.08 | 49.53 | −0.02 | −0.02 | −0.102 | 0.920 |

modulation of intra- and inter-brain phase coherence during joint attention relative to individual attention across the entire 1 s interval that was analyzed (see Figs. 4,5 and Fig. 6). Particularly strong increases of inter-brain phase coherence were observed 100 to 500ms after stimulus onset (see Figs. 5 and 6) in the delta frequency band and most pronounced at frontal to parietal sites (see Fig. 6). The strongest increase in intra-brain synchronization was also observed during the first 400 ms following stimulus onset in the delta frequency band (see Fig. 4). Increases in delta oscillations during individual EEG recordings have been observed during visual auditory stimuli detection tasks or high working memory load and have been related particularly to signal matching (Başar-Eroglu et al. 1992), which is highly relevant in our task. Also, this pattern replicates earlier studies that reported most pronounced effects in fronto-central regions for both within- and between-brain synchronization (i.e., PLI and IPC) at lower frequencies, namely in delta and theta frequency ranges during social interaction (Lindenberger et al., 2009; Delaherche et al., 2015; Sänger et al., 2012). Moreover, Sänger et al. (2012) found that within-brain synchronization (i.e., *PLI* and intra-brain strength) at lower frequencies was higher in leaders as compared to followers indicating modulation of intra-brain synchrony by musical roles, which may reflect that the role of the leader is associated with greater effort than the role of the follower. Using a graph theoretical approach, Müller and colleagues reported higher coupling strength and more connector hubs for these slow frequencies than for higher frequencies during joint musical improvisation on the guitar and suggested that slow frequency ranges generally play a bigger role in inter-brain synchronization than higher

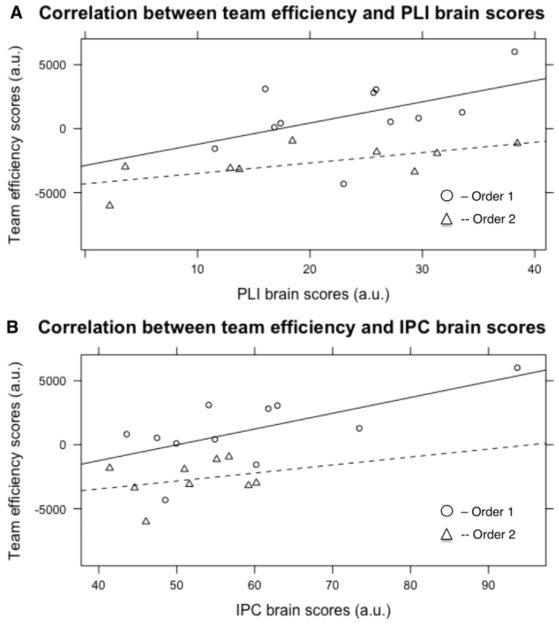


**Fig. 7.** Correlation between team efficiency and phase synchronization (*PLI* and *IPC*). Panel A. Correlation between team efficiency and *PLI* brain scores. Panel B. Correlation between team efficiency and *IPC* brain scores. The difference score between brain scores estimated by nr-PLS in the social condition and brain scores estimated in the individual condition was correlated with team efficiency scores. Circles indicate the session order with the individual condition first (Order 1). Triangles indicate the session order with the social condition first (Order 2). Solid line = regression line for session Order 1 Dashed line = regression line for session Order 2.

frequencies (Müller et al., 2013). Although inter-brain synchronization generally increased during joint attention, instances of reduced synchronization were observed as well (see Figs. 5 and 6). For example, we found fronto-central suppression of inter-brain phase synchronization at 8 Hz at 300 ms after stimulus onset (see Figs. 5 and 6). Attenuated power in the alpha frequency band during a joint finger-tapping task has been reported elsewhere (Konvalinka et al., 2014) and could in turn result in attenuated phase synchronization in the same frequency band. We interpret these general increases in local phase locking and inter-brain phase synchronization during joint vs. individual attention as a neural substrate of social facilitation.

The term social facilitation subsumes changes in behavioral performance associated with the passive or active presence of another person (Allport, 1920; Zajonc, 1965). Two mechanisms have been proposed to mediate social facilitation: On the one hand, automatic co-representation of the co-actors tasks (see Sebanz et al. (2003)) and on the other hand, a general increase in arousal, attention, or both (Dolk et al., 2011; Zajonc, 1965), which may reflect motivational aspects of social settings. Particularly for joint attention, the recruitment of reward-related neuronal circuits has been demonstrated (Pfeiffer et al., 2014; Schilbach et al., 2010). Our setting does not allow disambiguating the effects of task co-representation from the effects of increased attention/motivation. While participants searched two identical visual displays in the individual condition, they together searched one display in the social condition. At the beginning of the experimental session, most dyads used verbal communication to decide on splitting the visual display in halves, so that one participant would primarily search the left half and the other participant would primarily search the right half. In this situation, automatic co-representation of the co-actor's task (search left half and search right half of the display) should lead to task representation corresponding to the individual condition (search left half and right half of the display), thus, no difference between conditions should follow from task co-representation. Our results on intra-brain dynamics, namely, local phase synchronization within one brain, might be taken to support the view that social facilitation is expressed via heightened attention. Increased local phase synchronization has been suggested to play a major role in selective attention (Womelsdorf and Fries, 2007) and in response execution and inhibition (Müller and Anokhin, 2012). We observed changes in local phase synchronization from individual to social setting in both individual brains with localization and distribution patterns paralleling the activation patterns in inter-brain synchronization reported above (see Figs. 3–5), but exhibiting a different time course: the strongest increase in *PLI* was apparent 0 to 300 ms after stimulus onset in the delta frequency band, while it manifested most strongly 300–500 ms after stimulus onset for *IPC* (see Fig. 6). Importantly phase synchronization did not increase globally within individual brains during joint attention, as we did not observe any significant modulation of intra-brain phase coherence. *IPC* and *PLI* proved further similar in their correlations with behavior (see Fig. 7).

From a conceptual perspective, attention is a key factor to visual search success. In our paradigm, teams generally responded faster than individuals. This previously observed collaborative benefit has been hypothesized to go beyond the speeding effect expected when the number of searching eyes doubles (Brennan and Enns, 2014). We interpret this increased local phase synchronization during social setting, which we found paralleled by increases in inter-brain phase synchronization, to reflect a general heightening of attention during social setting and thus interpret these changes in neural phase synchronization as neural substrates of social facilitation.

Our second research question focused on a potential relationship between measures of phase synchronization during individual and joint attention and behavioral team performance. Here, our results suggest a link between local/inter-brain phase synchronization and behavioral team performance that has not been previously reported in the literature.

We hypothesized that increases in *PLI* and *IPC* during joint attention would both correlate with behavioral performance increases, a correlation that was indeed apparent in our data (compare Fig. 7). Increases in both *PLI* and *IPC* correlated positively with team efficiency. In a hierarchical regression with *IPC*, *PLI* and session order as predictors, *IPC* during individual and *PLI* during joint attention explained variance in behavioral team performance above and beyond the variance explained by the general learning effect (session order). The observed association between higher local phase synchronization during joint attention and larger performance gains from working as a team further corroborates our interpretation of increased neural phase synchronization as heightened attention underlying social facilitation. The more two players are susceptible to the social setting, the more their attention will increase in a social setting which on the behavioral level results in larger performance gains and at the neural level is reflected as increased local phase synchronization in both individuals. The finding that behavioral gains of working together are associated with higher inter-brain synchronization in particular during individual attention but not during joint attention might reflect that for inter-brain synchronization 'more does not equal better'. If indeed inter-brain synchronization reflects synchronization of cognitive processes, inter-brain synchronization and behavioral performance should increase in teams where both players co-represent their partner and build a joint forward model (see Sänger et al. (2011)). On the other hand, as pointed out earlier, the most effective strategy in the visual search task used here seemed to split the search screen between partners and to smoothly coordinate on the joint response. Brennan and Enns (2014) have shown that degree of friendship as well as distribution of cognitive load positively correlate with team efficiency. Relating our finding on *IPC* to these results might thus suggest that partners who during individual attention 'are on the same wavelength across brains' but do

not align their cognitive processes too closely during teamwork benefit most from working as a team in this task.

It is particularly interesting to point out that we assessed phase synchronization only during an initial period of individual and joint attention (first second of trials). However, local and inter-brain phase synchronization during this initial period explained variance in a pair's reaction time several seconds later (end of trials). This finding corroborates our hypothesis that modification of neural, inter-brain patterns by social context is of general nature and not restricted to stimulus presentation. Thus, increased inter-brain phase synchronization during joint attention does not reflect shared perceptual input only but social context as a general modifying factor of brain patterns.

In summary, we suggest that social context modulates intra-, as well as inter-brain dynamics in interacting individuals, possibly reflecting a general heightening of attention in social facilitation. At the level of intra-brain dynamics, this modulation is expressed as increased local phase synchronization. At the level of inter-brain dynamics, this effect appears to be boosted and reflected as increases in inter-brain phase coherence. *PLI* and *IPC* appear to be driven by similar cognitive processes, but at least to some extent both measures might capture different dimensions of these processes.

### *Limitations of the study*

As noted earlier, our study does not allow for clear and direct separation of task co-representation and increased attention (e.g., mediated via increased motivation) as the major forces underlying social facilitation. Also, pairs may have varied in how much they perceived the social condition as a passive or active social setting. The two subjects were exposed to the same stimulus array and knew they attended to it together. However, many dyads 'split' the search display between each other and potentially this may have weakened in some dyads the experience of co-action (active social facilitation) and instead provoked a feeling of audience (passive social facilitation), which may have limited the study's potential to maximize differences in intra- vs. inter-brain processes. Future studies using our collaborative visual search task may overcome this limitation by further differentiating explicitly between passive social facilitation (e.g. participants watch each other's individual tasks) and active social facilitation. Moreover, the similarities and differences in *PLI* and *IPC* patterns and thus the precise relationships between local phase synchronization in individual brains and phase synchronization between these brains need to be investigated further. It remains to be assessed to what extent the two measures capture different dimensions of similar or identical cognitive and neural processes.

## Conclusion and future directions

Taken together, we report increased inter-brain phase synchronization and increased local phase synchronization in joint attention relative to individual attention during a visual search task and interpret these findings as neural substrates of social facilitation. We further provide some evidence for the hypothesis that this social facilitation is in turn a result of heightened attention. Though local phase synchronization in one brain and inter-brain phase synchronization between brains may reflect similar cognitive processes, we found them to differ in explanatory power of behavioral performance. In our experimental setup session, order had a strong influence on behavioral performance and teamwork benefit and accounted for 50% of inter-dyad differences in benefit of working together. Remarkably, local and inter-brain phase synchronization combined explained an additional 25% of inter-dyad differences in teamwork benefit. As a result, inter-brain phase synchronization may be considered a useful tool in the study of neural team dynamics. Future research should further assess the use of local and inter-brain phase synchronization as sensitive measures of social facilitation or as measures to detect and predict promising team constellations. Dual eye tracking studies might be of particular interest to clarify if dyads indeed split the visual search space between each other and if spatially and/or temporally synchronized eye movements might serve as a major driver of inter-brain phase synchronization. Real-time dual eye tracking setups have been used recently to signal one person's social cues to his ore her interaction partner in the absence of any other non-verbal or verbal communication (Neider et al., 2010; Schilbach, 2015; Timmermans and Schilbach, 2014). Such setups allow for a high degree of experimental control and could be used to clarify the relation between eye movements, social gaze, and intra- and inter-brain synchronization dynamics within dyads. Another possible avenue to further disentangle the functional relevance of intra- and inter-brain dynamics for social interaction might lie within the field of psychiatry. Elsewhere, real-time dyad interaction paradigms have been suggested as a useful tool to study diseases that involve disturbances of social interaction, such as autism or schizophrenia (Schilbach, 2016). Potentially, intra- and inter-brain synchronization might be differentially altered in patient-control dyads during joint attention.

Furthermore, it would be interesting to actively manipulate inter-brain phase synchronization by means of non-invasive neural stimulation to gain more insight into the relationship between behavioral team performance and inter-brain phase synchronization patterns.

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# Neural Synchronization during Reciprocal and Parallel Interpersonal Action Coordination

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**Abstract**

Studies using EEG-hyperscanning (the simultaneous measurement of several subjects' EEG) have repeatedly revealed interpersonally synchronized patterns during interpersonal action coordination. Yet, consensus is lacking as to whether this inter-brain synchronization is an intrinsic feature of social interaction or primarily reflects similarities of the two interactors' motor output and perceptual input. In this study, we use a novel computer-game paradigm to disentangle the relative contributions of interpersonal interaction and input/output similarity to inter-brain phase synchronization during action coordination. By recording behavioral patterns during reciprocal coordination and replaying these recorded patterns in later trials, we can compare reciprocal interactive coordination to parallel non-interactive coordination that follows the same behavioral dynamics. Our results suggest that similarity of motor output and perceptual input is a major contributor to inter-brain phase synchronization, even in the absence of interpersonal interaction. Inter-brain phase synchronization, in particular in the alpha range in right centro-parietal electrode pairings, has previously been associated with interpersonal interactivity. Our results suggest that inter-brain phase synchronization at this frequency and location may more generally reflect the behavioral dynamics of a coordinated action. Behaviorally, subjects experienced reciprocal coordination as well as parallel coordination following the same behavioral dynamics as mutual teamwork. The results of our study suggest that interactive coordination may not necessarily differ, experientially or neurally, from parallel coordination that is characterized by the same coordination dynamics. More generally, our evidence supports the idea that inter-brain phase synchronization may be seen as a neural measure of coordination dynamics that embodies characteristic (motor) information about an interaction.

## 1 Introduction

Inter-personal action coordination is a prominent feature of human life. We pass salt at the dinner table and applaud our favorite soccer team when they navigate the difficult coordination problem of passing a ball back and forth among different individuals to score a goal. Joint action has been formerly defined as “any form of social interaction whereby two or more individuals coordinate their actions in space and time to bring about a change in the environment” (Sebanz, Bekkering et al. 2006, p.70) and *joint forward models*, mental representations of the actions to be performed by both the actor and her/his co-actor, have been put forward as its cognitive basis (Sänger et al. 2011, Vesper et al. 2016). But there are also instances of interpersonally coordinated actions that do not involve social interaction*:* Think of a smoothly functioning assembly line, where each worker performs their individual task exactly as instructed without having to be aware of the other workers’ tasks. Think of a dance performance, where a wall separates two dancers, who both dance the same choreography to the same music. To the audience, their performances appear as synchronized and perhaps even as interacting. These cases of inter-personal action coordination do not require two individuals to have a joint forward model of their actions, but rather to both have the same individual forward model of their own actions. We will refer to interpersonal action coordination that relies on interaction as *reciprocal coordination* and to action coordination without interaction as *parallel coordination*. In recent years, the idea ‘that social cognition is fundamentally different when we are in interaction with others’ (Schilbach et al. 2013, p.1) has gained increasing popularity (Sebanz, Bekkering and Knoblich 2006, De Jaegher et al. 2010). In light of this *interactive turn* in social neuroscience (Gallotti and Frith 2013), the present study intends to compare interactive interpersonal ncoordination and non-interactive interpersonal coordination at the neural level.

If interaction is to play a fundamental role in social cognition, what is the hypothesized function of interaction for social cognition? Several decades ago J.A. Scott Kelso formulated a *theory of dynamic patterns*, which postulates that human behavior is governed by the processes of self-organization (Kelso 1995). According to this theory, behavioral patterns are a result of the self-organized coordination of distinct, yet mutually coupled, systems made up of e.g. muscles, nerves or neurons. From this perspective, two interacting individuals become coupled through their behavioral interaction and the resulting dynamics that emerge from this interaction, the *coordination dynamics,* are at the same time constitutive of the coordination itself. Behavioral studies following this rationale have demonstrated emergent coordination dynamics in the motor behavior of two interacting participants e.g. when rocking in chairs or tapping their fingers (Konvalinka et al. 2010; Richardson et al. 2007) and developmental studies further highlighted the role of reciprocal interaction for the development of social cognition as such (Carpendale and Lewis 2004). In social neuroscience, more and more researchers have adopted this ‘second-person approach’ to social cognition that postulates that one misses a fundamental aspect of social interaction when studying social cognition from the spectatorial view only (Schilbach 2010, Gallotti and Frith 2013). Instead, the necessity to construe experimental paradigms that allow studying participants actively engaged in interaction from the ‘interactor’s perspective’ (Schilbach et al. 2013) has been

pointed out repeatedly (Kelso 1995; Konvalinka and Roepstorff 2012; Sebanz, Bekkering, and Knoblich 2006). Initial studies making use of innovative set-ups to study reciprocal real-time interaction e.g. with a virtual avatar have shown that different neural networks are recruited when initiating joint attention oneself as opposed to engaging in joint attention initiated by another (Schilbach et al. 2010).

But despite these recent advances a quote from Auvray and Rohde (2012) remains relevant: “One major open question for interactionist research on social cognition is the study of how the underlying processes are neurally implemented.“ (Auvray and Rohde 2012). *EEG-hyperscanning* (Babiloni et al. 2007) has gained popularity as a tool with the ability to shed light on the question of how neural mechanisms relate to coordination dynamics in social interaction (e.g., De Jaegher, Di Paolo, and Adolphs 2016; Konvalinka and Roepstorff 2012; Sänger, Lindenberger, and Müller 2011). Indeed, studies using this technique have revealed neural synchronized patterns between brains engaged in joint action (e.g., Lindenberger et al. 2009; Nadel 2014; Sänger, Müller, and Lindenberger 2012; Tognoli et al. 2007). Particularly, oscillations in centro-parietal connections have been frequently reported (Tognoli et al. 2007, Lindenberger et al. 2009, Astolfi et al. 2011, Sänger, Müller and Lindenberger 2012, Müller and Lindenberger 2014). In particular, right-lateralized, centroparietal coupling in the alpha range, the so-called ‘phi complex’ has been put forward as a ‘neuromarker for human social coordination’ (Tognoli et al. 2007). Notably, the phi complex has been repeatedly observed during imitation that involved moving the left as well as the right hand. Thus, the lateralization of the phi complex to the right hemisphere appears independent of motor behavior and instead might reflect the lateralization of mechanisms that support coordinated behavior. Specifically, the phi complex has been proposed to reflect ‘the influence of the other on a person's ongoing behavior’ (Tognoli et al. 2007, p.8190). Other authors associated oscillations in right centroparietal areas in a broader frequency range (5-15 Hz) with self-other integration (Novembre et al. 2016). Yet, it remains unclear whether these inter-brain synchronized patterns primarily reflect similarity of perceptual input and motor output or if they capture some other property that emerges only during reciprocal interaction. Partly, this is due to the paradigms chosen for EEG hyperscanning, which so far have mainly focused on reciprocal behavior (e.g., by investigating joint guitar play (Müller, Sänger, and Lindenberger 2013), imitation (Nadel 2014), joint finger-tapping (Konvalinka et al. 2014)), and on the comparison between cooperative and non-cooperative interaction (e.g., by investigating card game play (Babiloni et al. 2007), flight simulation (Astolfi et al. 2011) or visual search (Szymanski et al. 2017). Some studies have lent support to the hypothesis that inter-brain synchronized patterns primarily reflect similarity of input/output, for example, Dumas and colleagues have shown that mere interactional synchrony, regardless if intended or accidental, drives inter-brain synchronized patterns in the alpha-mu, beta and gamma frequency band. Other studies have supported the hypothesis that inter-brain dynamics capture aspects unique to social interaction, e.g., by showing differential brain activities between leaders and followers in a joint finger tapping paradigm (Konvalinka et al. 2014), during joint guitar play (Sänger, Müller, and Lindenberger 2013), and during conversation (Jiang et al. 2015). But these differences between leaders and followers do not

constitute conclusive evidence, since they are not necessarily tied to the interaction itself. Instead, these differences may reflect differential cognitive engagement for the social roles of following and leading. Here, we introduce a novel computer-game paradigm that enables us to compare inter-brain dynamics during reciprocal interpersonal action coordination with interaction (*reciprocal*) and during parallel interpersonal action coordination without interaction *(replay)* while keeping perceptual input and motor output highly similar in both conditions. We operationalize this dissociation by replaying trials previously recorded during reciprocal interaction. Thus, in *replay* subjects cannot interact with each other, but can only react to the same recording. However, the coordination dynamics contained in this recording reflect the signature of reciprocal coordination. By comparing the *reciprocal* condition to (a) the non-interactive *replay* condition with highly similar input/output and to (b) the non-interactive *alone* condition with less similar input/output, our novel paradigm disentangles the effect of interaction and similarity of input/output in interpersonally coordinated actions on inter-brain neural synchronized patterns. We further use a fourth *replay other* condition, where subjects supposedly hold two individual forward models that differ more from each other than in the *replay* condition, to test if small differences in two individual's mental action models impact inter-brain synchronized patterns.

Making use of this novel paradigm, the aim of the present study was to separate the specific contribution of interaction to interpersonal action coordination performance from general contributions reflecting the similarity of individuals' actions and percepts. Thus, we specifically addressed the following two research questions: (1) Is inter-brain phase synchronization sensitive to the presence of interaction in the sense that it reliably differs between reciprocal and parallel coordination? (2) Is inter-brain phase synchronization sensitive to changes in shared motor output, in the sense that it differentiates between conditions that differ in behavioral dynamics?

## 2 Material and Methods

### 2.1 Participants and Data Analysis

#### 2.1.1 Research Participants

Fifty-six healthy individuals participated in the study, forming a total of 28 non-overlapping pairs, 13 male-male pairs and 15 female-female pairs. As men and women display different interaction dynamics in conversation (Boker et al. 2011), we included only same-sex pairs in the study. The age of the participants ranged from 18 to 30 years (mean age = 25.23, SD = 3.43). All pairs were included in the behavioral data analysis. One male pair and one female pair had to be excluded from the EEG analysis due to a technical problem with data registration. Participants were randomly assigned within gender to pairs and did not know each other prior to the experimental session. All participants volunteered for the experiment, and gave their written informed consent prior to their inclusion in the study. The Ethics Committee of the Max Planck Institute for Human Development approved the study. The study was performed in

accordance with the ethical standards laid down in the 1964 Declaration of Helsinki.

### 2.1.2 Experimental Setup

At the beginning of each experimental session, participants filled out a battery of questionnaires that assessed overall intellectual ability (Raven Advanced Progressive Matrices, John C Raven 1962), personality (NEO Five-Factor-Inventory, Costa and McCrae 1992) and interpersonal skills (Circumplex Scales of interpersonal Values, Locke 2000). During the subsequent preparation for the EEG session, participants were placed on two chairs opposite each other and asked to engage in small talk. All pairs talked about study subjects and hobbies/interests for approximately ten minutes until the experimenter asked them to stop talking and to enter the EEG cabin. The two participants were comfortably seated back-to-back in the electromagnetically shielded EEG cabin. Each participant faced a computer screen placed on a table directly in front of them. Displays subtended 37° x 30° visual angle on a 19-inch computer monitor (screen resolution 1280 x 1024 pixels). Both subjects' right hands were comfortably placed on a joystick on their tables (see also Figure 1).

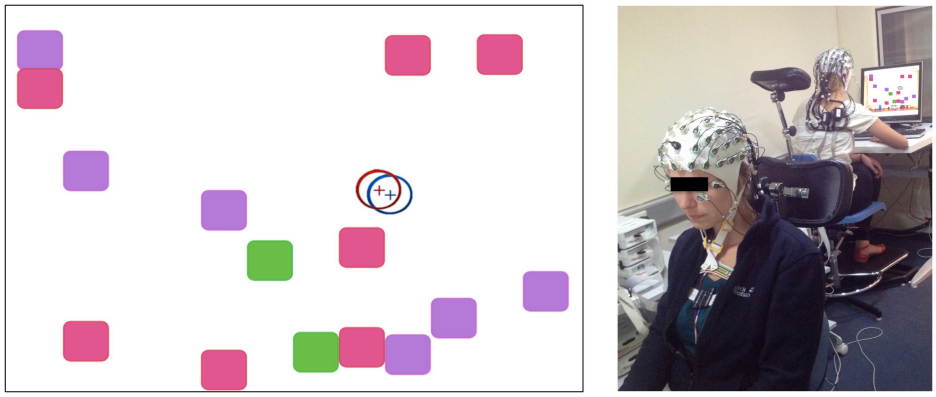

Figure 1. A. Example display of the paradigm ‚Stay with me'. B. Experimental set-up in the electromagnetically shielded cabin.

### 2.1.3 Paradigm 'Stay with Me'

The novel interactive virtual game 'Stay with Me' was specifically designed for this study and implemented in C++. Each 90-second-trial started with two circles (red/blue, with a distance of 400 pixels) displayed at the center of the screen; immediately squares began to fall and rise vertically across the screen (100x100 pixel, speed varies between 2-4 pixel/16ms, at any given point in time there were between 4 and 15 squares present on the screen). The participants' task was to (a) navigate the circles through the squares while (a) avoiding collisions with the squares and while (b) maximizing spatial overlap between

their circles (see Figure 1 B for an example display). Each participant controlled direction and speed of one circle (red/blue, diameter 100 pixel, speed = 1-4 pixel/16ms) by joystick. At the end of each trial, feedback on performance (number of collisions and circle overlap score[1]) was displayed in the upper right corner. Participants then indicated perception of control by button press. ('Who determined the course of the game'? 1= me, 5 = jointly, 9=my partner). One practice trial familiarized participants with joystick handling (40 seconds) before the study began.

The study consisted of 21 pseudorandomized trials divided into four conditions (*reciprocal*, *replay*, *replay other* and *alone*) designed to render our research hypotheses amenable to empirical scrutiny. In all four conditions, participants interact with their environment (the falling squares). *Reciprocal* is a case of reciprocal interpersonal action coordination, where each of two participants navigates his or her own circle each and also is free to interact with the other participant. *Replay* is a case of parallel interpersonal action coordination without interaction and thus the comparison between *reciprocal* and *replay* addresses our first research question. Identical to *reciprocal* in perceptual input, in *replay* both players see their own and the second circle on their screen. However, now this second circle is not their partner's active circle, but a circle that replays the circle movements recorded on an earlier *reciprocal* trial. Although this replayed circle is not reactive, the coordination dynamics contained in its movement reflect the signature of reciprocal coordination. Thus, in trials where I am replaying my opponent, if I respond to the same stimuli the same way, coordination dynamics are identical to the *reciprocal* trial that is being replayed.[2] In *replay,* both participants are always shown an identical recording: in 50% of replay trials both participants coordinate with the circle movements recorded from participant A, in 50% with the circle movements recorded from participant B, to balance 'me-replays' and 'partner-replays'. *Replay other* is also a case of parallel interpersonal action coordination, but different from *replay* in that the recording comes from a *reciprocal* trial from a different pair [3] and coordination dynamics are thus not endemic to the dyad, but different and more difficult to predict. While *replay* construes a case of parallel coordination where the participants are expected to hold highly similar mental forward models, participants might deal differentially with the altered coordination dynamics and thus hold less similar mental forward models during *replay other*. Comparing inter-brain synchronization between *replay* and *replay other* yields insight into its sensitivity to small alterations in mental models and behavioral dynamics. Finally, *alone* is a condition that is identical to replay and replay other in that there is no interaction between the participants. Additionally, behavioral

[1] Each second of perfect overlap is rewarded with 80 points. Points per second are prorated for partial overlap, with a linear decrease in points for partial overlap, down to a single point for one second with only a single pixel of overlap.

[2] Also the square environment is replayed from the reciprocal trial recorded earlier.

[3] The *replay other* recordings are identical for all subjects, in that they are always the same recorded circle movements from *reciprocal* trials of one and the same participant during piloting.

dynamics differ more between the participants. Analogue to the other three conditions, each participant is navigating one circle each, but in contrast they see no second circle on the screen and their only goal is to avoid collisions with squares. In *alone,* participants do not try to move their circles in unison and as a result motor output becomes less synchronized than in *reciprocal*, *replay* and *replay other*. Thus, a comparison between *alone* and the other three conditions addresses our second research question.

After the experiments, participants completed a post-questionnaire that assessed overall perceived difficulty and performance of self/partner. The questionnaire included funnel questions to explore if the participants had noticed manipulations to the degree of interaction (awareness of manipulation) or any irregularities they could not name (suspicion of manipulation) during any point of the experiment.

### 2.1.4 EEG Data Acquisition

The EEG was recorded with active 64 Ag/AgCl electrodes per person, placed according to the international 10–10 system, with the reference electrode at the right mastoid (actiCAP, Brain Products, Munich, Germany). Separate amplifiers (BrainAmp DC, BrainProducts, Munich, Germany) with separate grounds were used for each individual, linked to one computer. Vertical and horizontal electrooculograms (EOGs) were recorded to control for eye blinks and eye movements. All channels were recorded at a sampling rate of 5000 Hz. A 0.016–1000 Hz bandpass filter was used. Triggers were sent from the stimulus presentation computer to the EEG-recording system at trial onset and in subsequent 10s intervals. One stimulus presentation computer was connected to three synchronized screens for game presentation. Two screens were placed inside the cabin, whereas one control display was placed outside the EEG cabin to monitor stimulus or game presentation.

## 2.2 Behavioral Data Analysis

To test our second hypothesis, we first assessed similarity of movement and coordination performance across all four conditions to quantify differences in behavioral dynamics between conditions.
Objective coordination performance was measured as (a) number of collisions per trial (used as a proxy of coordination with the environment and) and (b) as circle distance (used as a proxy of partner coordination and a proxy of similarity of movement[4]). Subjective dyad performance was measured by post-trial

[4] In all conditions, circle distance was the distance between the two circles that were real-time controlled by the participants.

questions (see paradigm description) and by a funnel interview at the end of the experiment.

We used R (R-Development-Core-Team, 2008) and lme4 (Bates, 2015) to perform linear mixed effects analyses on the relationship between performance and condition. To test differences in circle distance (and thus approximate movement synchrony) between the four conditions, we constructed a linear mixed model with circle distance as the dependent variable, condition (*reciprocal*, *replay*, *replay other*, *alone*) and trial number (1:21; to control for potential training effects) as fixed effects, and dyad-level intercepts as random effects (distance ~ condition + (1 | dyad)). We then used multcomp (Hothorn, 2016) for post-hoc analyses of all condition contrasts within the model (*reciprocal – alone*, *replay* – alone, *replay other* – alone, *reciprocal – replay*, *reciprocal – replay other*, *replay – replay other*) with Bonferroni correction for multiple comparison. Visual inspection of residual plots did not reveal any obvious deviations from homoscedasticity or normality. P-values for the fixed effect in question were obtained by likelihood ratio tests of the full model with the effect in question against the model without the effect in question. P-values for all individual factor levels of the fixed effects were calculated from F statistics using Satterthwaite's approximation for denominator degrees of freedom. The tests on random effects were performed using likelihood ratio tests (both implemented in R statistical software using 'lmerTest'). To test for differences in coordination performance with the environment (number of collisions) between the conditions [5], we constructed a mixed model with log-transformed number of collisions as the dependent variable, condition (*reciprocal*, *replay*, *replay other*, *alone*) and trial number (1:21) as fixed effects, and considered subject-level intercepts nested within dyad as random effects (collisions ~ condition + (1 | dyad / subject)). Again, we calculated Bonferroni corrected simple effect comparisons of all condition contrasts within the model (*reciprocal – alone*, *replay – alone*, *replay other – alone*, *reciprocal – replay*, *reciprocal – replay other*, *replay – replay other*).

Our next analysis focused on effects of teamwork on performance. We assessed performance change (in number of collisions) for each individual between playing alone and playing reciprocally. We sorted the participants into the 'stronger' and 'weaker' player within their respective dyad, based on their average performance on *alone* trials. We then calculated the difference score between average joint performance and average individual performance for each player. We used a Welch dependent means t-test to examine whether performance changes differed systematically for stronger and weaker players within a dyad. To test for effects of condition on subjective performance ratings, we first used repeated measures ANOVA with rating of control as dependent, condition as independent variable and individual ID as error. We then performed post-hoc analyses for linear mixed model analysis with ratings as dependent

[5] We log-transformed the number of collisions to obtain heteroscedastic data.

variable, condition as independent variable and subject ID nested within dyad ID as random effect

## 2.3 EEG Data Analysis

### 2.3.1 Preprocessing

EEG data were filtered with a high-pass filter at 0.5 Hz and resampled at 1000 Hz. EEG activity was segmented into epochs of 10 s. Eye movement and artifact correction (head or body movements) was accomplished through independent component analysis (Vigário 1997) and semiautomatic visual inspection. Only artifact-free epochs were included in further analyses. To reduce the amount of data and to overcome the problem of volume conduction between neighboring electrodes, we selected 21 electrodes distributed across the entire cortex (international 10–20 system: Fp1, Fpz, Fp2, F7, F3, Fz, F4, F8, T7, C3, Cz, C4, T8, P7, P3, Pz, P4, P8, O1, Oz, and O2). This selection reduces a possible bias in functional connectivity findings produced by volume conduction, while still covering the entire cortex (cf. Lindenberger et al. 2009; Sänger, Müller, and Lindenberger 2012).

### 2.3.2 Synchronization Measures

To obtain a measure of inter brain synchronization, we transformed the EEG time series into a complex time-frequency signal by convoluting them with a complex Gabor wavelet (Lachaux, Rodriguez, Martinerie, & Varela, 1999) of cycle number $c = 5$ for frequencies from 2 to 20 Hz, in steps of 2 Hz (10 frequency values in total). The Gabor wavelet was computed following the equation:

$$G(t, f_c) = e^{-\frac{t^2}{2\sigma_t^2}} e^{-j2\pi f_c t},$$

where $t$ and $f_c$ denote time and the center frequency, respectively, $j = \sqrt{-1}$, and $\sigma_t = c/(2\pi f_c)$ sec, leading to a time wavelet length of $\lambda_t = 2\pi\sigma_t = c/f_c$ sec and to a spectral bandwidth of $2/\lambda_t$ Hz. The convolution was performed by multiplication in Fourier space, followed by the inverse Fourier transform (see DPtf_fft.m in Supplemental Materials). From this complex transform, we extracted the instantaneous phase time series and we computed the phase difference between electrodes *k* and *l* at trial *n*, time *t* and frequency *f,* being equal to:

$$\Delta\varphi_{kl}^{n}(t, f) = mod(\varphi_{k}^{n}(t, f) - \varphi_{l}^{n}(t, f), 2\pi)$$

Finally, we computed the inter-brain phase coherence, which represents the degree of constancy in phase difference between two electrodes measured from two brains simultaneously within a time window $T = 1$ sec, via:

$$IPC_{kl}(t, f) = \left| \frac{1}{N_T} \sum_{t_i}^{N_T} e^{j\Delta\varphi_{kl}^{n}(t_i, f)} \right|,$$

where $t_i$ stands for each one of the $N_T$ time points of the window $T$ (= 1s) and the time $t$ is at the center of the window. We included all possible pairs of the 21 electrodes chosen per subject in our analyses, adding up to 441 connections analyzed per frequency band and a total of 4410 connections analyzed per condition.

### 2.3.3 Statistical Analysis of Inter-brain Synchronization

We averaged connections within frequency bins and performed a Type II MANOVA with trial averages of the *IPC* frequency bands as dependent variables (1:10), and condition (*reciprocal*, *replay*, *replay other*, *alone*) and dyad ID (28 levels) as independent variables. We used model comparison using ANOVA between this model and a model with only dyad ID as independent variable to assess statistical significance. We further performed two linear mixed model analyses, the first model had *IPC* as the dependent variable, frequency (1:10) as fixed effect and by-dyad random intercepts (1:28), the second model additionally included condition (*reciprocal*, *replay*, *replay other*, *alone*) as a fixed effect. For the following analyses, we averaged *IPC* values within the 8Hz, 10Hz and 12Hz frequency bins for all possible pairs between Cz, C4, Pz, P4 and P8 to obtain *IPC* values for the phi range. We then performed three linear mixed model analyses, each with $IPC_{phi}$ as the dependent variable. The first model had condition (1:4) as a fixed effect and by-dyad random intercepts. The second model contained condition (*reciprocal*, *replay*, *replay other*, *alone*), circle distance and trial number (1:21). The third model additionally included number of collisions (log-transformed to obtain heteroscedastic data) as a fixed effect. We calculated multiple comparisons on the different condition contrasts and assessed statistical significance as described in detail under 'behavioral methods'.

## 3 Results

### 3.1 Behavioral Results

To assess differences in movement similarity and partner coordination performance between the four conditions, we subjected distance between both players' circles to linear mixed model analysis (see Methods section for a detailed description of the models used), which showed an effect of condition on distance ($\chi^2$ (3) = 1140.1, $p < 0.0001$). Relative to *alone*, circle distance decreased in all other three conditions (see Table 1). Notably, given the circle diameter of 100 pixels, circle distance was low even in *alone* (see Table 1 and Figure 2). Simple effect comparisons showed that *replay* and *reciprocal* differed on this measure of motor output similarity/partner coordination, yet with little over half a circle diameter this effect was very small ($\beta$ = –60.88, SE = 3.18, z = –19.15, $p < 0.0001$). *Replay other* and *reciprocal* differed to a similar extend in

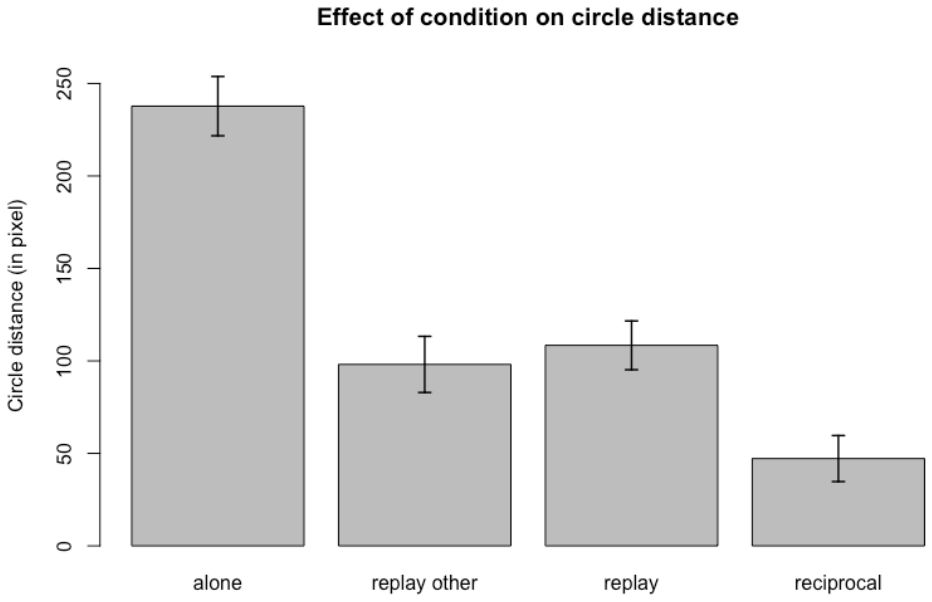


Figure 2. Results of a linear mixed model analysis for the effect of condition on circle distance.

motor output similarity/partner coordination ($\beta$ =–53.91, SE = 4.09, z = –13.18, $p < 0.0001$; see Table 1 and Figure 2), while we observed no difference between *replay other* and *replay* ($\beta$ = 6.97, SE = 4.33, z = 1.61, $p$ = 0.37.) Random effects accounted for 29.52% of variance in distance.

| Condition | B | SE | DF | t-value | *p*-value |
|---|---|---|---|---|---|
| Alone | 237.76 | 8.01 | | | |
| Reciprocal | –190.56 | 6.23 | 1032 | –45.07 | <0.0001 |
| Replay other | –139.65 | 7.59 | 1032 | –26.15 | <0.0001 |
| Replay | –129.34 | 6.60 | 1032 | –28.62 | <0.0001 |
| Trial number | –0.31 | 0.23 | 1032 | –1.37 | > 0.05 |

Table 1. Fixed effects estimated with linear mixed models grouped by individual for circle distance in pixel.

*Reciprocal*, *replay*, *replay other,* and *alone* also differed in coordination performance with the environment (measured as number of collisions). Linear mixed model analysis showed effect of condition on number of collisions (log-transformed) ($\chi^2$ (3) = 816.73, $p < 0.0001$). Coordination with the environment worsened in all three interpersonal conditions compared to *alone (see Table 2)*.

| Condition | B | SE | DF | t-value | *p*-value |
|---|---|---|---|---|---|
| Alone | 2.443 | 0.06 | | | |
| Reciprocal | 0.72 | 0.02 | 1312 | 30.84 | <0.0001 |
| Replay other | 0.59 | 0.03 | 1312 | 20.44 | <0.0001 |
| Replay | 0.78 | 0.02 | 1312 | 31.43 | <0.0001 |
| Trial number | –0.009 | 0.001 | 1131 | –6.80 | <0.0001 |

Table 2. Fixed effects estimated with linear mixed models grouped by individual for number of collisions (log-transformed).

Simple effect comparisons showed coordination with the environment was better during *reciprocal* than during *replay* ($\beta$ = 0.06, SE = 0.02, z = 3.52, $p <$ 0.005), but improved from *reciprocal* to *replay other* ($\beta$ = –0.097, SE = 0.02, z = –4.31, $p < 0.001$>) as well as from replay to *replay other* ($\beta$ = –0.16, SE = 0.02, z = –6.65, $p < 0.001$), yet again the size of this effect was small (see Table 2 and Figure 3). Random effects accounted for 51.25% of variance in log-

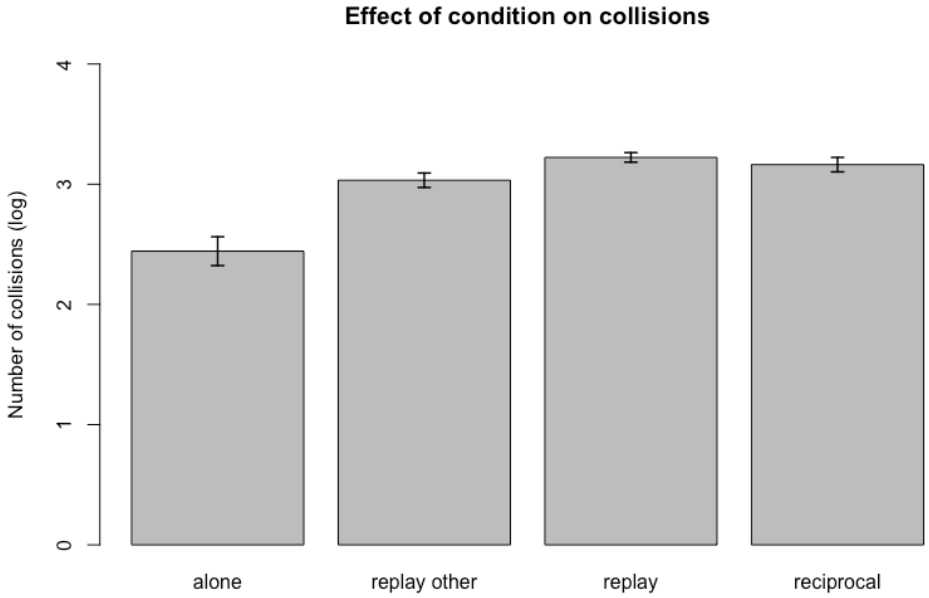


Figure 3. Results of a linear mixed model analysis for the effect of condition and trial number on log-transformed number of collisions.

transformed number of collisions (random intercept for dyad *alone* accounted for 49.44%, reflecting the fact that collisions for reciprocal trials were always identical for the subjects within one dyad). Interestingly, we observed an interaction between trial number and the difference between *reciprocal – alone*

($p < 0.001$), *reciprocal – replay* ($p < 0.05$), but not between *reciprocal* – replay other(all $p = 0.88$).

Taken together, behavioral dynamics followed the same general movement patterns in all four conditions. Between *reciprocal* and *replay* we observed small differences in partner coordination performance, motor output similarity and environment coordination performance. Accordingly, differences in inter-brain phase synchronization between *reciprocal* and *replay* would reflect either that inter-brain phase synchronization is sensitive to the presence of interpersonal interaction or that it is sensitive to small alterations of movement similarity and coordination performance. *Replay* and *replay other* did not differ in partner coordination performance (similarity of motor output), but differed in environment coordination performance. Thus, a difference in inter-brain phase synchronization between these two conditions might be taken as evidence that *IPC* is a very sensitive measure of coordination performance.

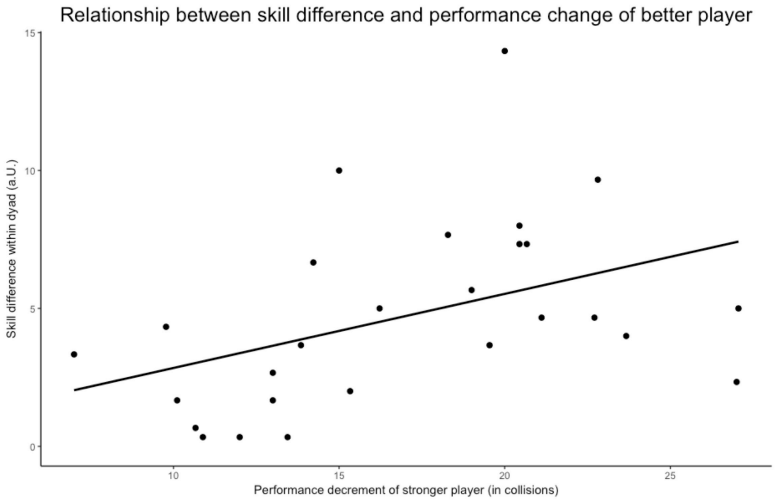


Figure 4. Effect of teamwork on coordination performance.

Next, we examined effects of teamwork on coordination performance (via number of collisions).[6]The difference scores between average joint performance and average individual performance for each player were positive for all subjects (reflecting the fact that the game as such was more difficult in the interactive conditions). A Welch two sample t-test showed a difference between these difference scores for weak and strong players ($t(52)= 3.22$, $p < 0.005$). Upon playing together, the stronger player's performance worsened from on average 13.44 collisions in *alone* to on average 30.37 in together, an average increase of 126%. The weaker player's average increase 67% (from 18.14

[6] We could only use number of collisions for this analysis. In contrast to circle distance only number of collisions remains a relevant measure of coordination performance in the *alone* condition.

collisions in *alone* to 30.37 in together). Interestingly, we observed a correlation between the difference in skill level within a team (difference score of both player's average performance in *alone*) and the stronger player's average performance decrement on reciprocal trials (Pearson correlation: r = 0.43, t(25) = 2.375, $p < 0.05$; see Figure 4). On the other hand, there was no correlation between the difference score and the weaker player's average performance decrement on reciprocal trials (Pearson correlation: r = –0.21, t(25) = –1.09, $p = 0.29$).

Next, we investigated the participant's subjective experience during the three interpersonal conditions. A repeated-measure ANOVA with rating of control as dependent, condition as independent variable and individual ID as error, showed a differential effect of condition on subjective performance ratings ('Who determined the course of the game?' (1-9), 1 = me, 5=mutual, 9 = partner) (F(2) = 32.59, $p < 0.0001$). Post-hoc analyses for a linear mixed model

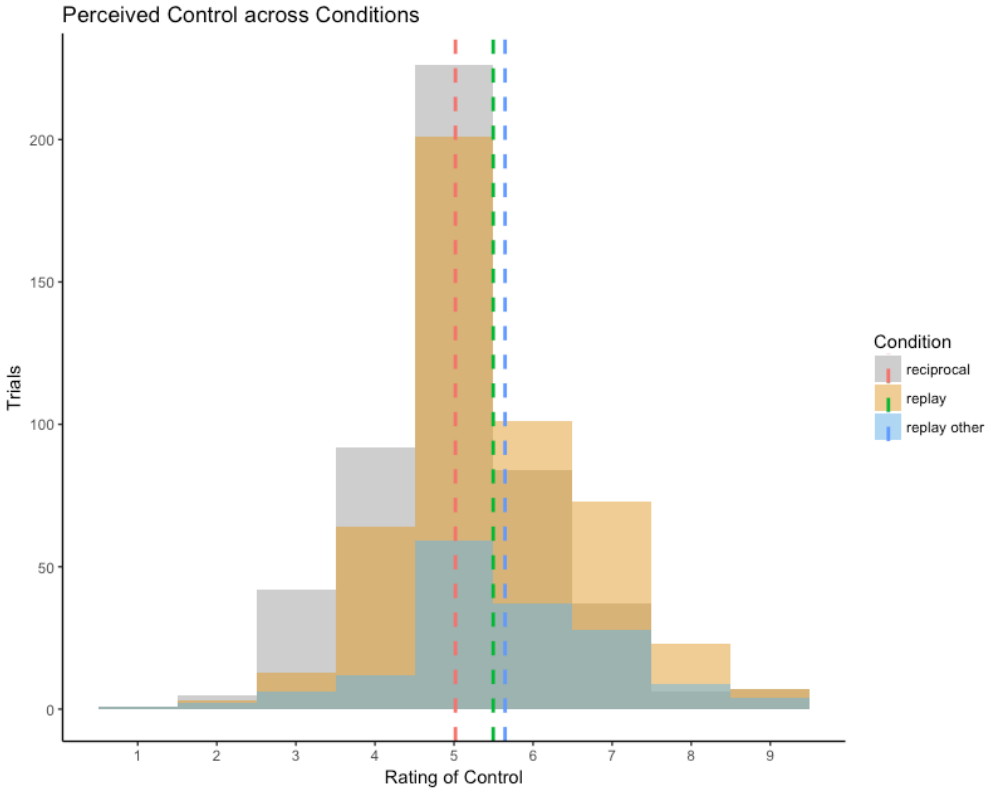


Figure 5. Histogram of the ratings of control across conditions registered at the end of each interactive trial. Dotted lines represent average rating per condition.

with ratings as dependent variable, condition as independent variable, and subject ID nested within dyad ID as random effects showed systematic differences in ratings of control for all condition contrasts. (*replay – reciprocal*: b= 0.46, SE = 0.08, z = 5.75, $p < 0.0001$; *replay other – reciprocal*: $\beta = 0.74$, SE = 0.10, z = 7.18, $p < 0.0001$; *replay – replay other*: $\beta = -0.28$, SE = 0.11, z = –2.57, $p < 0.05$). Notably, in all three conditions, performance was

overwhelmingly rated as ‘mutual’ (mean *reciprocal* = 5.01, mean *replay* = 5.44, mean *replay other* = 5.65; see Figure 5).

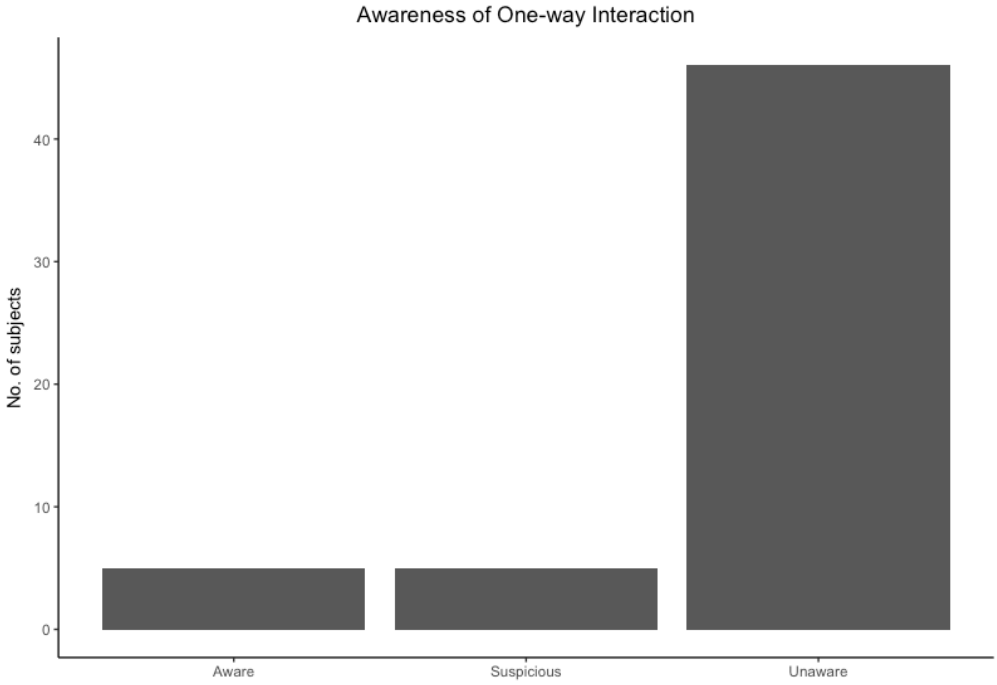


Figure 6. Histogram of results from funnel interview, which was used to assess awareness of the experimental manipulation (introduction of one-way coordination).

As part of the post-questionnaire funnel interview, we assessed if the participants had noticed the replay-manipulation and thus the fact that in almost every other trial they did not interact with each other. Out of 56 participants, 46 did not mention any awareness of manipulation at all (see paradigm description for details on these questions). In fact, many participants were very surprised when the experimenter revealed to them that they had played with recordings of their partner’s performance. A very typical reaction was ‘Oh! I thought my partner was just stupid sometimes (and had wondered why.)’. Five subjects reported suspicion of manipulations and five subjects reported awareness of the manipulation (see Figure 6). The ten subjects who reported suspicion/awareness did not belong to the same five dyads and displayed no apparent common characteristic.

### 3.2 EEG Results

Visual inspection of the grand average across pairs showed pronounced differences between the ten different frequency bins, with only marginal variation between conditions (see Figure 7). Differences between cortical areas within each frequency bin were much more fine-grained (see Figure 8). For this reason, we averaged connections within frequency bins and performed a Type

II MANOVA with trial averages of all ten *IPC* frequency bands as dependent variables, and condition and dyad ID as independent variables. Model comparison using ANOVA between this model and a model with only dyad ID as independent variable showed no effect for condition on the *IPC* ensemble ($F(30,1419) = 0.76$, $p = 0.82$). Dyad ID on the other hand showed a strong effect on the ensemble of *IPC* frequency bins ($F(250, 4800) = 5.30$, $p < 0.0001$, Pillai's trace = 2.16), that was strongest for the frequency bins 8Hz – 14Hz ($R^2$ for: 20Hz = 0.20 18Hz = 0.20; 16Hz = 0.20; 14Hz = 0.30, 12Hz = 0.32, 10Hz = 0.38; 8Hz = 0.29; 6Hz = 0.09; 4Hz = 0.02; 2Hz = 0.02). Given this strong effect of dyad on the *IPC* values, we used linear mixed models with by-dyad intercepts to assess a potential relation between *IPC* and conditions.

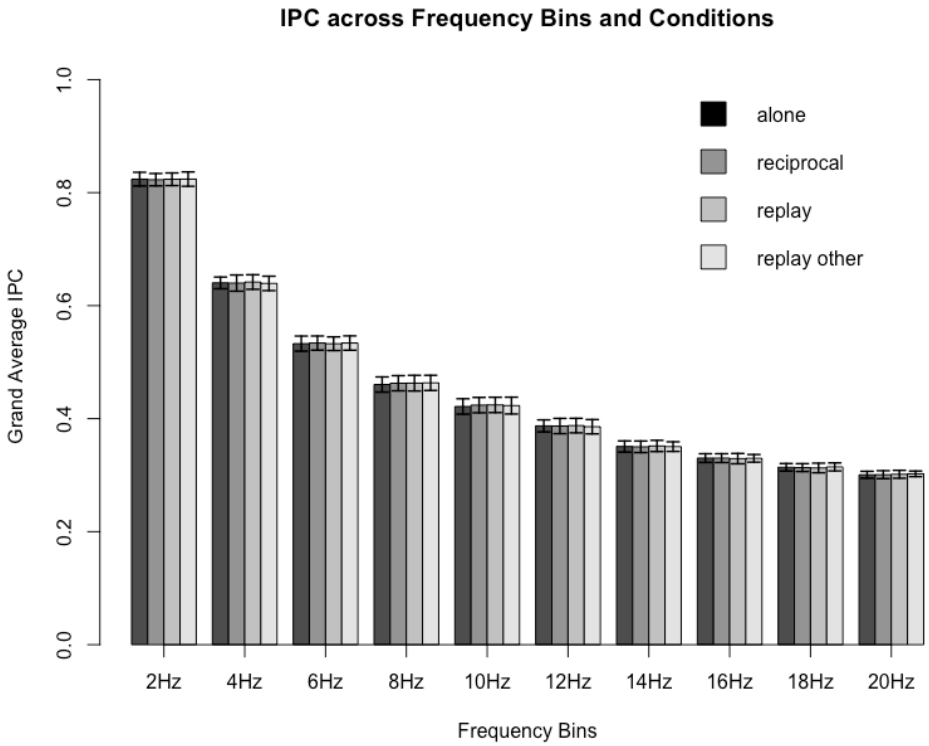


Figure 7. Grand average *IPC* values per frequency bin and condition.

Linear mixed model analysis with frequency as fixed effect and with dyad ID as random effect validated the pronounced difference in *IPC* between frequency bins apparent in Figure 7 ($\chi^2(9) = 28825$, $p < 0.000$, and see Table 3) and also the apparent similarity within frequency bins between conditions: when adding condition as a fixed effect to the model, model fit did not increase ($\chi^2(3) = 1.50$, $p = 0.69$). Based on the literature on hyperscanning and social interaction (Tognoli et al. 2007; Dumas et al. 2010), we narrowed our analysis of *IPC* to the phi frequency range and region, and averaged right parieto-parietal connections

(all possible combinations between electrodes Cz, C4, Pz, P4 and P8) across

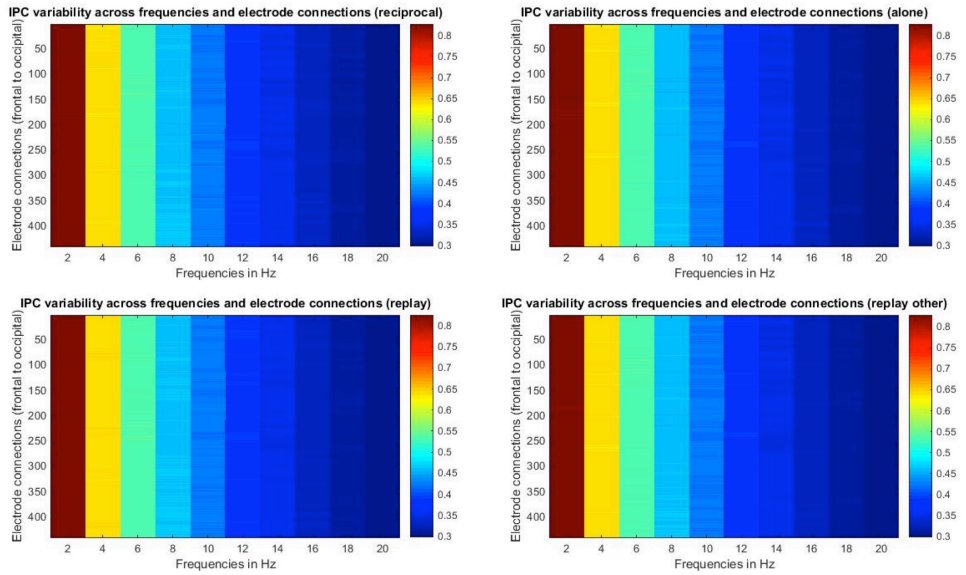


Figure 8. Grand average IPC values for each electrode connection, frequency bin and condition. color = IPC value.

the 8Hz, 10Hz and 12Hz frequency bins. A mixed model with condition, distance and trial number as fixed effects and subject ID nested in dyad ID as random effect showed an effect of distance on $IPC_{phi}$ ($\chi^2(1) = 7.10$, $p < 0.01$; see Figure 9) that disappeared when not controlling for condition. Simple effect comparisons showed that the effects of both distance and of condition for the contrast *reciprocal – alone* (z = 3.09, p = 0.01) were statistically significant. The other condition contrasts exhibited trends at most (*reciprocal – replay*: z = 1.76, *p* = 0.28; *reciprocal – replay other*: z = 2.35, *p* = 0.08; *replay – alone*: z = 2.36, *p* = 0.08; *replay other– alone*: z = 1.45, *p* = 0.46; *replay – replay other*: z = 0.96, p = 0.77, see Figure 9). Adding number of log-transformed number of collisions as a fixed effect to the model did not improve model fit ($\chi^2(1) = 1.37$, p = 0.24).

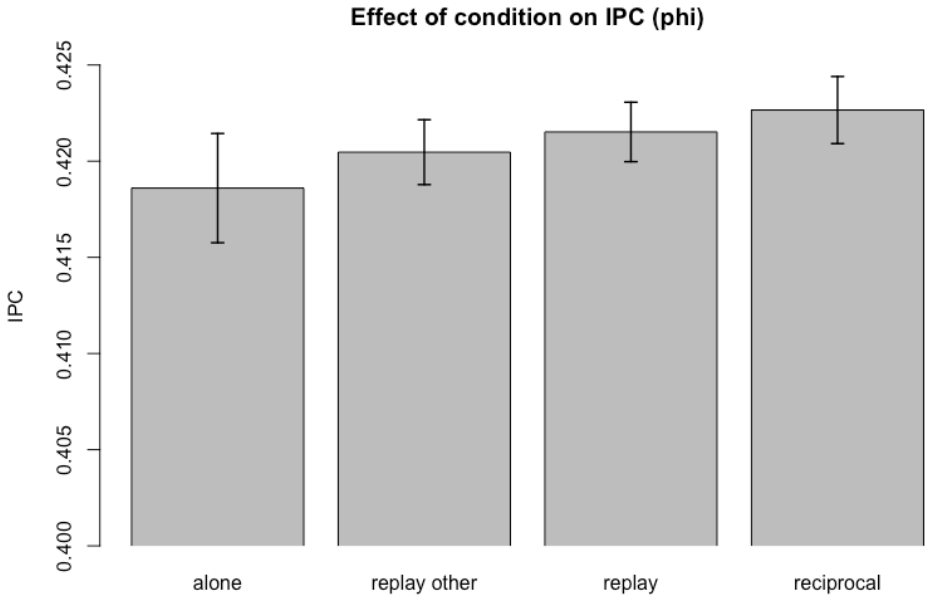


Figure 9. Results of a linear mixed model analysis for the effect of condition,on IPC in the phi range (8-12Hz, right centro-parietal electrode connections).

| Frequency Bin | *IPC* estimate | SE | DF | t-value | p-value |
|---|---|---|---|---|---|
| 2Hz | 0.82 | 0.0006 | | | |
| 4Hz | –0.18 | 0.0006 | 5303 | –280 | <0.0001 |
| 6Hz | –2.90 | 0.0006 | 5303 | –444 | <0.0001 |
| 8Hz | – 3.61 | 0.0006 | 5303 | –552 | <0.0001 |
| 10Hz | –4.00 | 0.0006 | 5303 | –614 | <0.0001 |
| 12Hz | –4.36 | 0.0006 | 5303 | –669 | <0.0001 |
| 14Hz | –4.72 | 0.0006 | 5303 | –726 | <0.0001 |
| 16Hz | –4.93 | 0.0006 | 5303 | –759 | <0.0001 |
| 18Hz | –5.10 | 0.0006 | 5303 | –784 | <0.0001 |
| 20Hz | –5.22 | 0.0006 | 5303 | –803 | <0.0001 |

Table 3. Fixed effects estimated with linear mixed models grouped by dyad for the effect of frequency on IPC.

## 4 Discussion

The main goal of the present study was to disentangle the impact of interaction and input/output similarity on inter-brain phase synchronization.
The field of EEG hyperscanning has mainly focused on reciprocal behavior (e.g., by investigating joint guitar play (Müller, Sänger, and Lindenberger 2013) or joint finger-tapping (Konvalinka et al. 2014)) and on the comparison between cooperative and non-cooperative interaction (e.g., by investigating card game play (Babiloni et al. 2007), flight simulation (Astolfi et al. 2011) or visual search (Szymanski et al. 2017). To our knowledge, no EEG-hyperscanning study has yet compared reciprocal interpersonal coordination to parallel interpersonal coordination. Further, the EEG-hyperscanning field as a whole has been criticized for a lack of studies that include adequate control conditions and address one fundamental assumption of the hyperscanning method: 'What aspects of social interaction do inter-brain synchronized patterns reflect and how do they advance our understanding of the neural mechanisms of social cognition?' (Konvalinka and Roepstorff 2012; Szymanski et al. 2017)
With the present study, we introduce the novel gaming paradigm 'Stay with Me' that aims to exert high control on perceptual input and motor output while comparing interpersonal action coordination with interaction to interpersonal action coordination without interaction. In this game, subjects navigate a circle through a square environment and have to coordinate their circle's movement path with a second circle. We operationalized the dissociation of input/output similarity and interaction by a 'replay' manipulation: instead of seeing their own circle and the other player's circle on their screens, both players saw their own circle and the circle (movements) recorded during a previous trial of reciprocal interaction during an identical square environment. Although in this *replay* condition subjects could solely follow and not interact with the recording, the movement paths of both players' circles remained coordinated, as both were driven by the same, recorded circle path. Also, the coordination dynamics of these replayed paths contained the signature of the previous, reciprocal coordination. We then compared subjective experience, coordination performance and inter-brain phase synchronization between the replayed trials and the original reciprocal trials. Surprisingly, 46 out of 56 subjects reported no awareness that in every other trial there was no reciprocal interaction between themselves and their partner (see Figure 6). However, subjects did perceive trials during parallel coordination as more controlled by their partner than they perceived trials during reciprocal coordination (see Figure 5). The absolute size of this effect was small and despite being unable to influence their partner's actions on the screen, subjects consistently perceived parallel coordination as teamwork (see Figure 5). We interpret this finding in that the information contained within the coordination dynamics is essential to the subjective experience of reciprocity and mutuality. The finding that subjects perceived also

*replay other*[7] as teamwork, but as slightly more partner-controlled than *replay* supports this interpretation and further suggests that coordination dynamics embody task-specific and dyad-specific information and both information types contribute to the subjective experience of reciprocity and mutuality.

Our primary interest in the analysis of inter-brain synchronization was the comparison between *reciprocal* and *replay*, the comparison between reciprocal interpersonal coordination and parallel interpersonal coordination. Our behavioral measures showed that the two conditions differed very subtly in motor output similarity/partner coordination (measured as circle distance, see Table 1) and in coordination performance with the environment (measured as number of collisions, see Table 2). Interestingly, we did not observe any difference in inter-brain phase synchronization between *reciprocal* and *replay* across the entire span of EEG frequencies analyzed (see Figure 7), nor when focusing specifically on right centro-parietal connections in 8-12Hz ('the phi complex as a neuromarker of human social coordination', Tognoli et al. 2007; see Figure 9). This null result suggests that inter-brain phase synchronization is not generally sensitive to the presence of interaction, neither that it is generally sensitive to very small differences in motor output similarity between two individuals.

Striking in our results on inter-brain synchronized patterns was a strong exponential relation between *IPC* and frequency bin ($\chi^2(9) = 28825$, $p < 0.0001$) with lower frequencies showing systematically stronger *IPC* values across all frequencies and all cortical areas (see Figure 7 and Figure 8). The *IPC* values in the delta and theta range were in all conditions – interactive and non-interactive, inter-personal and intra-personal – comparable to the values reported in the literature for joint action (Dumas et al., 2010; Müller et al., 2013). As perceptual input and motor output are comparable between all four conditions, this observation suggests that input/output similarity and EEG frequency exert a strong influence on inter-brain phase synchronization, while the effect of social interaction on *IPC* is comparatively small at most.

Besides this effect of frequency on *IPC*, we also observed an effect of dyad ID on *IPC*. Thus, the frequency at which inter-brain patterns are most synchronized between two persons engaged in a similar task is characteristic of a dyad. This finding suggests sharpening the current focus in the EEG hyperscanning literature (Tognoli et al. 2007) to detecting dyad-specific markers/networks of coordination.

Right parieto-central connections in the frequency range of 8-12Hz have been repeatedly suggested to play a pivotal role in social cognition and particularly in inter-brain phase synchronization during social interaction/coordination (Dumas et al. 2010; Nadel 2014; Tognoli et al. 2007). Interestingly, we observed the most pronounced effect of dyad ID on *IPC* for 8-14Hz. In a next step, we

[7] In the *replay other* condition we replayed circle movements that were recorded during reciprocal interaction of a different dyad.

focused our analysis on connections in the phi frequency band (8-12Hz) and region (right centro-pariteal) for a more fine-grained analysis of the relationship between interaction and *IPC*. Mixed model analysis revealed an effect of distance on $IPC_{phi}$ when controlling for condition (see results section for more details) and a systematic effect of condition on $IPC_{phi}$ for the comparison *alone – reciprocal*. Interestingly, the contrasts *reciprocal – replay other* and *replay – alone* were much closer to representing systematic trends ($z = 2.35$, $p = 0.08$ and $z = 2.36$, $p = 0.08$) than the contrasts *reciprocal – replay*, *replay – replay other* and *replay other – alone* ($z = 1.76$, $p = 0.28$; $z = 0.96$, $p = 0.77$ and $z = 1.45$, $p = 0.46$). Thus, the two condition comparisons (*Reciprocal – replay other, replay – alone*) that differ more on our behavioral measures also show a greater tendency for differences in $IPC_{phi}$. These tendencies and the effect of distance may be taken to support the interpretation that $IPC_{phi}$ is not modulated by the presence/absence of interaction, but rather by differences in input/output similarity or, in other words, by differences in behavioral dynamics. Thus, our results on *IPC* could be interpreted in that neural inter-brain phase synchronization, particularly between right centro-parietal connections at 8-12Hz, captures the behavioral/coordination dynamics of an interaction. We find coordination performance and thus motor output (as circle distance and number of collisions) to be sensitive to the type of coordination (reciprocal vs. parallel). Coordination dynamics are embedded within the motor output of all interactors of a coordinated action. Thus, our finding that inter-brain phase synchronization is mainly driven by input/output similarity does not stand in contrast to the hypothesis that inter-brain phase synchronization represents a neural implementation of coordination dynamics (Auvray and Rohde 2012), because any neural mechanism that is to represent coordination dynamics needs to represent motor output at a very fine-grained level.

On a complementary note, we also investigated changes in coordination performance between playing alone and playing as a team. In an earlier study from our lab, we had observed that teams with the strongest changes in *IPC* from individual to joint attention, also exhibited the strongest performance increases from individual work to teamwork. Another interesting finding on inter-team differences in performance comes from Bahrami and colleagues (2010). These authors observed that teamwork only improved individual performance when both partner's skills with respect to the task were similar (e.g., visual acuity for a visual discrimination task). Instead, for teamwork with a partner of lower skill, the better partner's performance deteriorated. We tested if this mechanism held true in our study. Due to the conceptualization of our paradigm, the inter-personal conditions were more difficult than the intra-personal *alone* condition, as the individual condition only necessitated coordination with the environment, while the interactive conditions necessitated coordination with the partner's circle as an additional factor. Thus, in our paradigm, all dyads' performances were worse than the players' individual performances. However, the degree of performance decrement was correlated

with the skill difference between the two players in a dyad. The more two partners in a dyad differed in their coordination skills, the more the better player's performance deteriorated, while there was no systematic effect on the weaker player's performance change. Thus, pairing a very good player or a slightly good player with a weak player would in both cases drag the dyad's performance towards the level of the weak player. At the same time, we observed no systematic (learning) benefit for a weaker player paired with a much better player. Thus, in our paradigm, one should aim to pair individuals with comparable skill level to obtain overall the highest possible level of performance.

As a limitation, we acknowledge that perceptual input and motor output of the parallel and reciprocal conditions were similar but not identical. MoreoverHence, differences in interbrain synchronization continue to be open to a number of different explanations. , specifically synchronicity of motor output has been associated with increases in inter-brain synchronization. The current study was not designed to examine synchronicity of motor output specifically and future studies should overcome this limitation in particular. On the contrary, mIn addition, similarity in motor output was generally quite high across all experimental conditions, including the alone conditions. The lack of a condition in which participants are (a) not interacting and (b) their motor output is very different from one another might have prevented us from detecting differences and commonalities in inter-brain synchronized patterns at additional frequencies and regions previously observed during action coordination, namely in the theta, delta or higher alpha frequency range (Lindenberger et al. 2009; Müller, Sänger, and Lindenberger 2013; Müller and Lindenberger 2014; Novembre et al. 2017).

## 5 Conclusion and Future Directions

In the present study, inter-brain phase synchronization between two individuals engaged in an action coordination task did not differ reliably between a condition that afforded reciprocal coordination, and a condition in which such coordination was rendered impossible. Specifically, our results showed no difference in *IPC* between reciprocal coordination and parallel coordination. Our study was specifically designed to separate input/output similarity from reciprocal interaction. Thus, its findings may serve as a cautionary note not to overemphasize the importance of reciprocal interaction for inter-brain synchronization. This finding has further implications for the hypothesis that inter-brain synchronized patterns reflect joint forward models (Sänger, Müller and Lindenberger, 2012), as it may suggest that IPC does not always differentiate between forward models formed during reciprocal interpersonal coordination and forward models formed during parallel interpersonal coordination. Thus, while inter-brain synchronized patterns may reflect multiple individuals' forward models that both encode their own as well as their partner's

actions, it remains unclear in howfar reciprocity and ‘jointness’ might be reflected in these models. Instead, inter-brain synchronized patterns might reflect commonalties in multiple individuals’ forward models. During joint action one’s partner’s actions are likely incorporated into one’s forward model. Thus during joint action commonalities in individual forward models are likely to increase. Hence increases in inter-brain synchronization would be generally expected for during joint action. However, we suggest that it is rather the commonalities than the ‘jointness’ of two individuals’ forward models that is reflected in inter-brain synchronization. Consequently, inter-brain synchronization can also be observed during parallel, non-interactive coordination.

Future studies using paradigms where the action plans of two partners differ substantially may shed light on this question. For example, one could construe scenarios in which two interacting individuals have different action goals while assuming their partner to hold the same goal. This would create a scenario where the action plans of two partners differ substantially and the relation between congruency of action plans and inter-brain phase synchronization could be studied, in particular during the period in which individuals revise their actions plans to make them more compatible to one another.

On a different note, our finding that the better player’s performance deteriorates towards the level of the weaker player is highly relevant with regard to the controversial debate on team composition and performance benefits of teamwork in organizational psychology (Bell 2007; Hall and Weaver 2001). The finding suggests that pairing low-performance with high-performance individuals deteriorates overall performance levels rather than improving them. Yet, it is unclear if and how this finding translates to real-life instances of coordination performance, e.g., project teams in corporate environments (Wuchty, Jones, and Uzzi 2007). Future research on performance benefits/decrements in teamwork should investigate performance tradeoffs for weaker and stronger individuals separately, while controlling for differences in skill level between the individuals in one team.

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frontiers in Human Neuroscience

ORIGINAL RESEARCH
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# Frequency-Unspecific Effects of θ-tACS Related to a Visuospatial Working Memory Task

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Working memory (WM) is crucial for intelligent cognitive functioning, and synchronization phenomena in the fronto-parietal network have been suggested as an underlying neural mechanism. In an attempt to provide causal evidence for this assumption, we applied transcranial alternating current stimulation (tACS) at theta frequency over fronto-parietal sites during a visuospatial match-to-sample (MtS) task. Depending on the stimulation protocol, i.e., in-phase, anti-phase or sham, we anticipated a differential impact of tACS on behavioral WM performance as well as on the EEG (electroencephalography) during resting state before and after stimulation. We hypothesized that in-phase tACS of the fronto-parietal theta network (stimulation frequency: 5 Hz; intensity: 1 mA peak-to-peak) would result in performance enhancement, whereas anti-phase tACS would cause performance impairment. Eighteen participants (nine female) received in-phase, anti-phase, and sham stimulation in balanced order. While being stimulated, subjects performed the MtS task, which varied in executive demand (two levels: low and high). EEG analysis of power peaks within the delta (0.5–4 Hz), theta (4–8 Hz), alpha (8–12 Hz), and beta (12–30 Hz) frequency bands was carried out. No significant differences were observed between in-phase and anti-phase stimulation regarding both behavioral and EEG measurements. Yet, with regard to the alpha frequency band, we observed a statistically significant drop of peak power from pre to post in the sham condition, whereas alpha power remained on a similar level in the actively stimulated conditions. Our results indicate a frequency-unspecific modulation of neuronal oscillations by tACS. However, the closer participants' individual theta peak frequencies were to the stimulation frequency of 5 Hz after anti-phase tACS, the faster they responded in the MtS task. This effect did not reach statistical significance during in-phase tACS and was not present during sham. A lack of statistically significant behavioral results in the MtS task and frequency-unspecific effects on the electrophysiological level question the effectiveness of tACS in modulating cortical oscillations in a frequency-specific manner.

**Keywords: working memory, central executive, cortical oscillations, theta phase synchronization, tACS**

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## INTRODUCTION

In line with Baddeley's multicomponent model (Baddeley and Hitch, 1974; Baddeley, 2000), working memory (WM) refers to the temporary storage as well as manipulation of information for goal-directed behavior. Neurobiological and neuroimaging findings over the last decades have conveyed the idea that WM might depend on specific anatomical structures, including prefrontal

and parietal regions (Goldman-Rakic, 1988; Curtis and D'Esposito, 2003; Bledowski et al., 2009). However, the premise of anatomical localization as a solid theoretical basis for a system as pervasive as WM has been criticized (Baddeley, 2012). Consequently, in recent years progressively more studies have shifted their interest from an exclusive "where" approach toward the "when" of WM processes and/or components (Sauseng et al., 2005, 2010; Jensen et al., 2007; Klimesch et al., 2010; Roberts et al., 2013; Roux and Uhlhaas, 2014). But which mechanisms characterize the temporal dynamics of WM? How does the brain simultaneously orchestrate activity between distant neural networks?

An answer to these questions may come from research conducted on cortical oscillations, a phenomenon ubiquitous in the human brain. Brain oscillations in different frequency bands have proven crucial for attentional as well as perceptual processes (Vanrullen and Dubois, 2011). Oscillations within the theta frequency band in particular have been associated with a wide range of behavioral processes, such as orienting reflex, attention, arousal, and memory, conditioning and learning, including binding and information processing mechanisms (Buzsáki, 2005). Similarly, enhanced oscillatory activity at delta frequency during cognitive tasks may be an indicator of attention and task demand (Harmony et al., 1996; McEvoy et al., 2001; Müller et al., 2009), as well as of response production and inhibition (Müller and Anokhin, 2012; Lavallee et al., 2014). In contrast to delta and theta frequency, alpha and beta rhythms show tendencies to reduce or to desynchronize during perceptual and memory tasks (Pfurtscheller and Lopes da Silva, 1999).

The synchronization of frequency-specific oscillatory activity between remote cortical networks may be understood as a 'fingerprint' of neural computations necessary for cognitive processes (Siegel et al., 2012). Oscillations ranging from lower (0.05 Hz) to higher frequencies (500 Hz) have been associated with specific cognitive/behavioral states (Wang, 2010) and synchrony within, as well as between, frequency bands has been reported to underlie process binding and large scale integration in general (Varela et al., 2001; Uhlhaas et al., 2008; Klimesch et al., 2010). Interestingly, there seems to be a relationship between the extension of functional integration and the synchronization frequency, i.e., lower frequencies, such as theta (4–8 Hz) and alpha (8–13 Hz) enable long-range fronto-parietal interactions, whereas higher frequencies (e.g., gamma, 30–200 Hz) seem to be particularly suitable for local, short-range integration (von Stein and Sarnthein, 2000).

With regard to WM maintenance, a recent review of EEG, MEG, and ECoG studies proposed distinct functional roles for neural oscillations at theta, alpha and gamma frequency. Gamma-band activity might be involved in maintaining WM information, whereas theta oscillations seem to play a key role in the temporal organization of sequentially ordered WM items (Roux and Uhlhaas, 2014). According to the inhibition-timing hypothesis (Klimesch et al., 2007), event-related synchronization in the alpha frequency band reflects top–down inhibitory control and timing processes of task-irrelevant cortical regions. On the other hand, event-related desynchronization indicates a gradual release of inhibition (Klimesch et al., 2007). Nonetheless, alpha oscillations have not only been associated with inhibitory processes of task-irrelevant material but also executive control of behavior and active task-relevant processing (Palva and Palva, 2011). Very little is known about the role of oscillations in the actual manipulation of WM content. Within Baddeley's multicomponent model, the modality-free central executive would be responsible for online manipulation as well as temporal coding or sequencing of WM content, updating of information, interference control, and also attentional and monitoring processes (Smith and Jonides, 1999). Thus, reluctance to investigate the central executive arises from the complications posed by its fractioned and distributed nature (Baddeley, 2012).

Nonetheless, a direct involvement of fronto-parietal theta phase coupling in central executive control mechanisms of WM has been suggested (Sauseng et al., 2005, 2010; Mizuhara and Yamaguchi, 2007). This interregional synchrony may even constitute an electrophysiological signature of the fronto-parietal control network (Dosenbach et al., 2008); an idea that is consistent with the finding that theta phase coupling is generally more spread across the brain compared to phase synchronization within the gamma range (Buzsáki, 2006). Such a spread may ensure the simultaneous activation of distinct local assemblies, each synchronized in the gamma band (Fell and Axmacher, 2011). Since most studies conducted so far on the topic of WM functioning have been correlational, the question of causality remains unsolved: is fronto-parietal theta phase synchronization a mere by-product of executive control in WM or does it have a causal function in "gating" the temporal window of integration?

One possible way of addressing this question is the use of transcranial alternating current stimulation (tACS), a relatively new and promising tool within the field of non-invasive brain stimulation which remains to some extent controversial (Kunz et al., 2016; Rjosk et al., 2016). TACS, the external application of weak sinusoidal electrical currents, is believed to entrain intrinsic cortical oscillations (Antal and Paulus, 2013) and may thus pave the way to investigate causal relationships between cortical oscillations and cognition. In contrast to direct current (DC), alternating current (AC) is not constant but switches polarity between anode and cathode with a sinusoidal waveform. *In vitro* and *in vivo* animal studies have suggested periodic modulation of transmembrane potentials (neural excitability) and entrainment of ongoing neural rhythms (shifts in spike-timing and firing) as key mechanisms of tACS (Fröhlich and McCormick, 2010; Reato et al., 2013).

However, the precise mechanisms of tACS are still debated: a recent tACS-fMRI study suggested that tACS does not necessarily cause its strongest effects underneath the stimulation electrodes, but in anatomically distant, yet functionally connected regions (Cabral-Calderin et al., 2016). Frequency-specificity has been reported in various empirical studies (Feurra et al., 2011; van Driel et al., 2015; Santarnecchi et al., 2016), even though there also is evidence for the method's frequency-unspecific effects (e.g., Brignani et al., 2013). Comparing pre- and post-stimulation EEG recordings, the application of tACS within participants' individual alpha peak frequency (iAPF), led to a frequency-specific amplitude enhancement of endogenous oscillations

(Zaehle et al., 2010). Neuling et al. (2013) replicated this finding and showed that the alpha amplitude enhancement outlasted the duration of stimulation for at least 30 min. Recently, Kasten et al. (2016) reported aftereffects of α-tACS up to a duration of 70 min. A study conducted by Polanía and colleagues has been particularly interesting with regard to the role of theta oscillations in the maintenance of WM. The authors applied θ-tACS with varying phase-lag between left frontal and parietal regions (return electrode: Cz). Reaction times (RTs) during a delayed letter discrimination task were shorter when fronto-parietal stimulation was 'synchronized,' whereas participants' performance deteriorated in the 'desynchronized' condition (Polanía et al., 2012).

The importance of this result for our understanding of the neural mechanisms orchestrating WM and the uncertainties about the effects of tACS on neuronal processing motivated the current study.

With this study we aimed to replicate the results on the importance of theta oscillations for WM performance reported by Polanía et al. (2012). We applied the same stimulation protocol used by Polanía and colleagues with a different WM paradigm, namely a visuospatial match-to-sample (MtS) task originally designed by Griesmayr et al. (2014). In contrast to Polanía et al. (2012) we controlled for additional factors that might drive performance changes, i.e., direction of current flow (Thut et al., 2017) as well as current intensities.

We hypothesized that similarly to the study by Polanía et al. (2012) fronto-parietal in-phase tACS at 5 Hz would enhance participants' performance, whereas anti-phase stimulation would similarly deteriorate their performance. We expected a particularly pronounced effect at high levels of executive demand. Moreover, we assumed that these behavioral effects would be in line with electrophysiological changes of EEG peak power values within the theta frequency band. Specifically, we hypothesized that EEG theta power would be enhanced upon active tACS (independently of the type of stimulation applied, in-phase or anti-phase) compared to sham. Of note, EEG power enhancement as an effect of tACS has been previously reported in other empirical studies (Zaehle et al., 2010; Neuling et al., 2013). In order to be able to detect possible effects in other frequency bands, we did not limit our analysis to the theta frequency band only, but also considered delta (0.5–4 Hz), alpha (8–12 Hz), and beta (12–30 Hz) frequency bands. We further hypothesized that each participant's theta peak power, as measured before stimulation during resting EEG, would shift closer to the stimulation frequency after receiving tACS compared to sham.

# MATERIALS AND METHODS

## Participants

A total number of 18 healthy subjects aged 20-29 years ($M = 25.2$, $SD = 2.96$) were recruited for the present experiment. Sample exclusion criteria included: left-handedness, age below 20 or above 29 years, history of severe medical and/or psychiatric conditions, pharmacological treatment with centrally acting drugs, non-removable metal parts of the head or implanted electronic devices, acute infection/discomfort. Furthermore, to ensure experimental blinding, only subjects being naive to transcranial electrical stimulation methods were included (Ambrus et al., 2010).

The study was approved by the ethics committee of the Deutsche Gesellschaft für Psychologie and was performed in agreement with the Declaration of Helsinki. Participants' informed written consent was acquired. The experiment was conducted in the EEG laboratories of the Max Planck Institute for Human Development in Berlin and all subjects were monetarily compensated according to local standards. Each subject was invited to three experimental sessions, which were scheduled at least 5 days apart from each other.

## Experimental Design

As illustrated in **Figure 1**, the experiment consisted of three components: first, participants' EEG was recorded before stimulation during a resting condition followed by 7 min of the delayed MtS task. Next, stimulation was turned on for 26 min. During the stimulation, participants engaged in the MtS task for 14 min and afterward completed a simple motor task for 10–12 min. Finally, stimulation was turned off and EEG was recorded again during a resting condition followed by 7 min of the MtS task. Overall, each experimental session lasted approximately 1.5–2 h. As a replication of the study by Polanía et al. (2012), sessions with different stimulation conditions were counterbalanced using a Latin square design (see Experimental Procedure).

## EEG Recording

EEG was recorded from 18 recording sites (i.e., Fp1, Fpz, Fp2, F7, F3, Fz, T7, C3, C4, T8, P7, P3, Pz, P4, P8, O1, Oz, and O2) using active Ag/AgCl electrodes mounted in an elastic cap and placed according to the international 10–20 system, with the reference electrode at the right mastoid (actiCAP, Brain Products, Munich, Germany). In order to control for eye blinks and movements, the vertical and horizontal electrooculogram (EOG) was measured. All channels were recorded with a sampling rate of 1000 Hz and a bandpass filter of 0.01-250 Hz. Electrode impedance was kept below 10 kΩ throughout the entire EEG recording.

## Experimental Procedure

In order to rule out between-subject differences in executive control prior to stimulation, all participants completed a 1.5 h testing session 1 week before the actual experimental sessions started. During this testing session, participants completed a short version of the Raven Advanced Progressive Matrices test (Heller et al., 2006) and three different computerized short versions of complex span tasks, i.e., operation span, symmetry span, and rotation span (Foster et al., 2014), which served as measures of WM capacity. Taking into account the scores on the test battery, subjects were then pseudo-randomly assigned to one of three groups to ensure that groups did not differ in any parameter other than stimulation order. As shown in **Table 1** and identical to previous work by Polanía et al. (2012), each group consisted of six subjects (three female). In

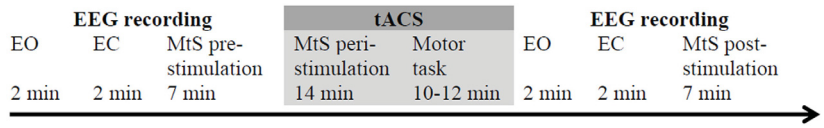


**FIGURE 1 |** Experimental design. The time course of experimental phases is presented. EC, eyes closed; EO, eyes open; MtS, match-to-sample task.

**TABLE 1 |** Orthogonalized cross-over design.

| | Sequence of stimulation | | |
|---|---|---|---|
| **Sessions** | **Group 1 (six participants)** | **Group 2 (six participants)** | **Group 3 (six participants)** |
| 1 | 5Hz_0° | 5Hz_180° | Sham |
| 2 | 5Hz_180° | Sham | 5Hz_0° |
| 3 | Sham | 5Hz_0° | 5Hz_180° |

*All 18 participants received in-phase, anti-phase, and sham stimulation. However, there were three different possible orders. The experimental design is a replication of the design used by Polanía et al. (2012).*

order to control for the sequence of stimulation conditions, each group received in-phase, anti-phase, and sham stimulation in a different order, resulting in a Latin square repeated measures design. In further analysis, the stimulation conditions (in-phase/anti-phase/sham) were treated as a within-subject factor. **Figure 2** illustrates the three experimental conditions: (1) in-phase condition (tACS at 5 Hz with a relative phase difference of 0°), (2) anti-phase condition (tACS at 5 Hz with a relative phase difference of 180°), and (3) sham condition (tACS at 5 Hz with a relative phase difference of 0° and a stimulation duration of 30 s). For all three conditions, the current was linearly ramped up until the intensity of 1 mA was reached and linearly ramped down to 0 mA at the end of stimulation. Stimulation was applied in a single-blind manner, i.e., subjects were not aware whether they received active tACS or sham stimulation.

All sessions took place in an acoustically and electromagnetically shielded cabin. To avoid line-frequency interference, all devices inside the cabin were battery-operated. After attachment of the EEG and tACS electrodes, the EEG recordings of the resting condition started with 2 min eyes open and 2 min eyes closed.

## Experimental Task

A delayed MtS task, adapted from Griesmayr et al. (2014), was used to evaluate two outcome measures of WM performance, i.e., RTs and percentage of accurate responses (**Figure 3A**). A 6 × 6 grid of gray boxes was presented at the center of a screen (19″ LCD monitor, visual angle of 9.2° × 9.2°, distance to screen: 0.8 m) using E-Prime 2.0 Professional software. Some of the boxes were colored in red, and the subjects' task consisted in mentally flipping the red boxes on the black vertical axis and keeping this new arrangement in mind after the grid disappeared. Executive demand of WM could either be low, i.e., only one red box, or high, i.e., three red boxes had to be flipped and remembered. After a 2000 ms delay period, a probe stimulus appeared. In 50% of the trials the probe was correct (match) and in 50% of trials it was not correct (non-match). The probe remained for 2000 ms. Participants were asked to indicate with their right index or right middle fingers via button press whether the probe matched the encoding stimulus or not (left arrow key for 'correct,' right arrow key for 'incorrect'). Inter-trial intervals were randomly jittered between 1100 and 1500 ms, with a fixation cross in the middle of the screen. There were 240 trials in total (60 trials pre-stimulation, 120 trials peri-stimulation, and 60 trials post-stimulation). Whereas 50% of all trials were characterized by low executive demand (low load), the other half represented high executive demand trials (high load). The order of presentation was randomized. The black/gray grid during the delay period served the purpose of avoiding color afterimages. Participants were instructed to respond as fast as possible, while maintaining accuracy. Participants completed the MtS task during 7 min before stimulation started, during 14 min while being stimulated, and during 7 min after stimulation had been switched off. A training block was carried out at the beginning of the experiment, until participants achieved performance scores above chance.

## Motor Response Task

The motor response task was implemented according to Polanía et al. (2012) in order to exclude the possibility of motor cortex stimulation via the Cz return electrode, which could have been responsible for improvements in RT. The task consisted of a red circle appearing in one of four positions which were horizontally spaced on a gray screen and permanently marked. There was a black vertical axis drawn in the middle. Subjects were instructed to press either the left arrow key or the right arrow key (using the same fingers as in the experimental task), depending on whether the red circle appeared to the left or to the right of the vertical axis, respectively. The task consisted of four blocks of 120 trials each. The sequence of circles followed a pseudorandom order, where circles were presented with the same frequency in each position and never in the same position in two subsequent trials. Subjects' response terminated the current trial. Participants completed the task during 10–12 min (depending on their performance) while being stimulated (see **Figure 3B** for an example stimulus).

## Electrical Stimulation

Transcranial alternating current stimulation was applied via two rubber electrodes (5 cm × 5 cm; Neuroconn, Ilmenau, Germany) attached to the head underneath the EEG recording cap, using a battery-operated stimulator system (DC-stimulator

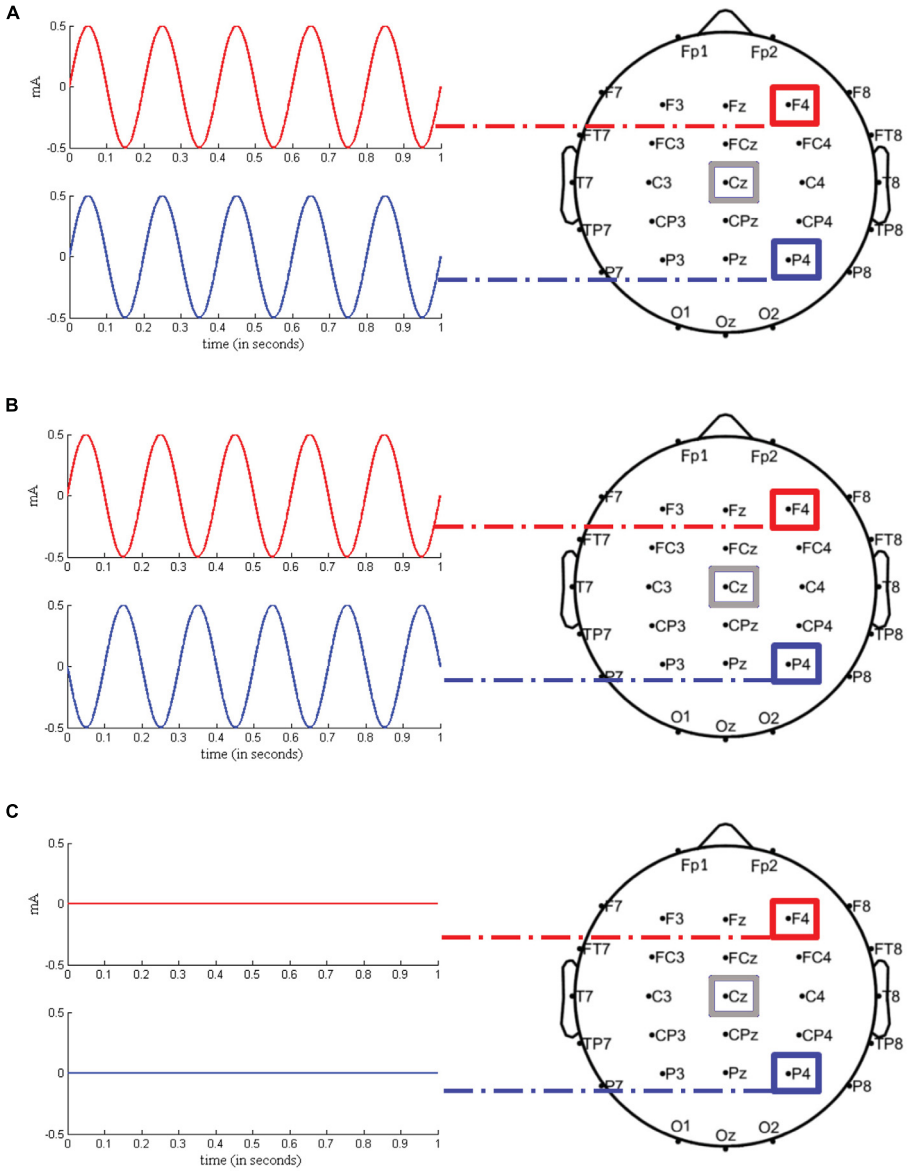


**FIGURE 2 |** Experimental stimulation setups. **(A)** In-phase condition. Transcranial alternating current stimulation (tACS) at a frequency of 5 Hz was applied over right frontal (F4) and right parietal (P4) regions, with a 0° relative phase angle. The return electrode was located over Cz. **(B)** Anti-phase condition. tACS at a frequency of 5 Hz was applied over the same regions as in **(A)**, with a 180° relative phase angle. **(C)** Sham condition. The current was gradually ramped in during 15 s at the beginning of the stimulation phase and then gradually ramped out during 15 s until 0 mA was reached. Stimulation setups were adapted from Polanía et al. (2012) and modified respectively.

plus, Neuroconn, Ilmenau, Germany). The target electrodes were placed over the right prefrontal (F4) and parietal (P4) cortices, with the return electrode at Cz. Given that a multi-channel stimulator system was used, each target electrode could be connected to one independent channel. Thus, in order to maintain stimulation conditions equal, both cables of the corresponding return channels were electromechanically manipulated, resulting in one single merged cable for the return electrode at Cz (see **Figure 4**). In line with results from Griesmayr et al. (2014), the stimulation frequency was 5 Hz

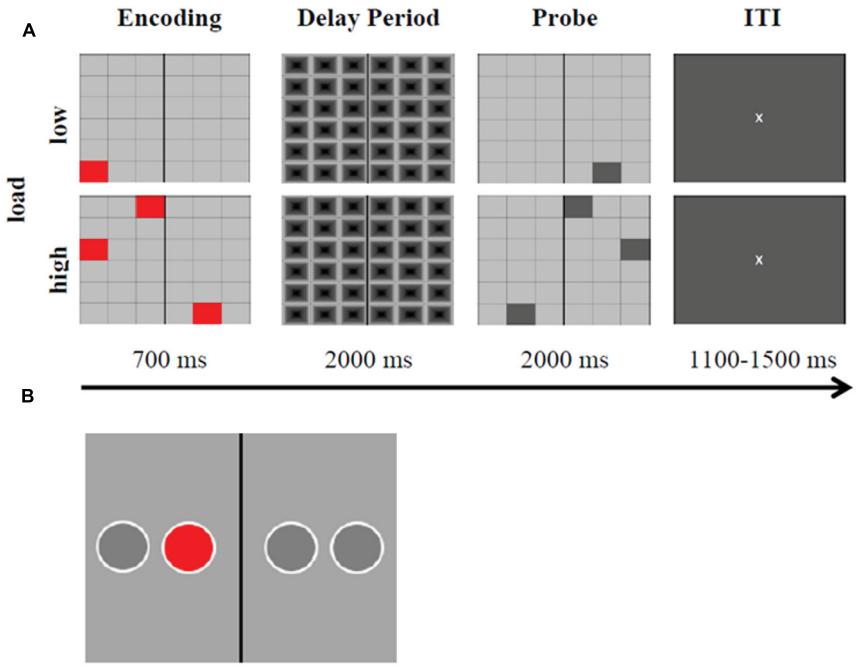


**FIGURE 3 |** Experimental task and motor response task. **(A)** Representation of the delayed visuospatial match-to-sample task (MtS). Time course with corresponding stimulus material during low and high load, both match and non-match trials are displayed. ITI, inter-trial interval. The MtS was adapted from Griesmayr et al. (2014) and modified respectively. **(B)** Example stimulus of the motor response task. The red circle appeared in each of the four positions randomly. While being stimulated (in-phase, anti-phase, or sham) subjects were instructed to indicate via button press whether the circle appeared to the left or to the right of the vertical black axis. RTs were measured. The task was adapted and modified from Polanía et al. (2012).

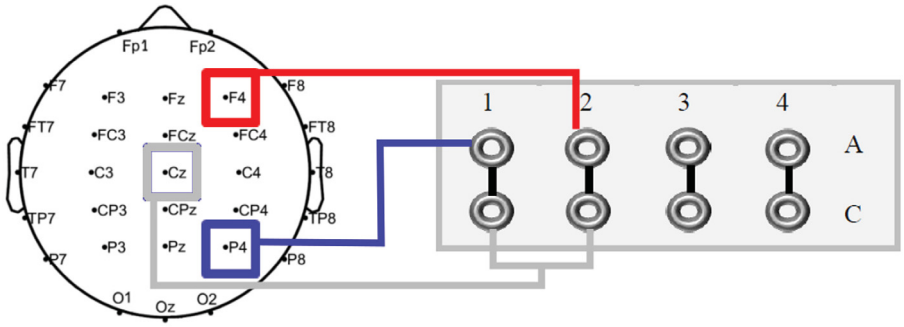


**FIGURE 4 |** Schematic outline of the multi-channel DC stimulator. Both active electrodes (F4 and P4) were connected to two independent channels. For the return electrode at Cz a cable was electromechanically soldered.

(within the theta range). A sinusoidal waveform was applied, without DC offset. Impedance was kept below 10 kΩ. In the first and last 15 s of stimulation, the AC was ramped in and out, respectively. According to standard blinding protocols, current amplitude and frequency were the same in the sham condition as in the experimental conditions, with the difference that AC was only applied for 30 s and afterward turned off automatically in sham. The possibility of phosphene induction within the theta frequency range is rather low and unlikely (Turi et al., 2013). In fact, none of the participants reported phosphenes, neither during the experimental piloting nor during the experimental sessions. Stimulation intensity was set to 1 mA (peak-to-peak), with a total stimulation duration of 26 min for each experimental session. As applied in previous tACS studies

(e.g., Neuling et al., 2013), an adaptation of the questionnaire on adverse effects by Brunoni et al. (2011) was used for debriefing.

## Data Analysis

### Behavioral Data Pre-processing and Analysis

Behavioral data was pre-processed using MATLAB R2014b (The MathWorks, Inc., Natick, MA, United States). For the posterior analysis of RTs, invalid trials were excluded, i.e., RTs > 2000 ms as well as error trials. Subsequently, outliers (> ±2 SD) were removed. As suggested by Baayen and Milin (2015), the proportion of removed data for each data distribution did not exceed 5%. Next, a Shapiro–Wilk parametric hypothesis test of composite normality was run. As expected, none of the distributions was normally distributed. Therefore, RTs were log-transformed. Mean accuracy rates were calculated for each subject during each stimulation condition (in-phase/anti-phase/sham) and for each load condition (low/high).

In order to test if participants were able to tell whether they were actively stimulated or sham stimulated, we conducted a chi-square test. The two categorical variables were STIMULATION (in-phase/anti-phase/sham) and SUBJECTIVE SENSATION (stimulation perceived/no stimulation perceived). Besides, in order to rule out behavioral performance improvements caused by motor cortex stimulation, we calculated a one-way repeated measures (RM) ANOVA on log-transformed RTs during the motor response task [within-subject factor: STIMULATION (in-phase/anti-phase/sham)].

We further conducted a 3x3x2 RM ANOVA on log-transformed RTs as well as accuracy rates assessed during the MtS task. The three within-subject factors were TIME(pre/peri/post), STIMULATION(in-phase/anti-phase/sham), and LOAD(low/high). The factor TIME was included in order to account for a possible learning effect during each experimental session.

### EEG Data Preprocessing and Analysis

Preprocessing of the electrophysiological data was carried out for resting EEG with eyes closed, using BrainVision Analyzer 2.1. The sequence of preprocessing steps was partly adapted from Miller et al. (2015). First, data were re-referenced to common average. Data were filtered, using a Butterworth zero phase filter (low cut-off: 0.5 Hz, high cut-off: 70 Hz, Slope: 24 db/Oct, Notch: 50 Hz). Next, an ocular correction ICA (independent component analysis) was performed to correct artifacts caused by eye movements and muscle activity. Data were then manually inspected for remaining eye and muscle artifacts. A fast Fourier transformation (FFT) with a 10% Hanning window (frequency resolution 0.488 Hz) was applied to the data. For all further statistical analysis MATLAB R2014b (The MathWorks, Inc., Natick, MA, United States) and SPSS 20.0 (IBM, Corp., Armonk, NY, United States) were used.

An exploratory EEG analysis of power peaks within the delta (0.5–4 Hz), theta (4–8 Hz), alpha (8–12 Hz), and beta (12–30 Hz) frequency bands was carried out. For all electrodes, peaks of spectral power were calculated algorithmically by determining the maximum amplitude within each frequency band.

A 2x3x18 RM ANOVA was run for each frequency band. The three within-subject factors were PRE_POST, STIMULATION (in-phase/anti-phase/sham), and ELECTRODE.

A region of interest (ROI) was defined consisting of the following electrodes: Fz, F8, Pz, P8, and Oz. These EEG electrodes were the ones located within the immediate vicinity of our stimulation electrodes. We expected an EEG power increase in both the in-phase and the anti-phase condition, as the tACS mechanism remains identical in both stimulation conditions. Both conditions (in-phase and anti-phase) only differ with respect to timing. During in-phase tACS, F4, and P4 receive stimulation simultaneously. During anti-phase stimulation, F4 and P4 receive stimulation with a time lag (180° relative phase angle). The measured EEG power post stimulation only reflects local power changes, i.e., power increase/decrease of underlying neural populations. Hence, an EEG power analysis does not take into account the timing aspect of stimulation, but changes in EEG power can be expected in active tACS (in-phase and anti-phase) compared to sham (Zaehle et al., 2010; Neuling et al., 2013). Therefore, we computed two reduced 2x2x5 RM ANOVAs (PRE_POST, STIMULATION, ROI). The within-subject factor STIMULATION in these analyses comprised the levels in-phase/sham and anti-phase/sham, respectively (Supplementary Figure 1 shows the non-linear effect of stimulation which justifies the use of a 2x2x5 ANOVA).

Mauchly's test of sphericity was applied to every analysis and Greenhouse–Geisser or Huynh-Feldt corrections were performed when sphericity was violated. Subsequent *post hoc* tests were Bonferroni corrected.

In a further step, individual $\Delta\theta$ (the difference between the stimulation frequency of 5 Hz and each participant's peak frequency within the theta range) was analyzed in order to determine the individual theta peak shift toward or away from the stimulation frequency after being stimulated. For this purpose, we first computed theta peak power algorithmically on an individual level before as well as after tACS. Next, we determined the specific theta frequency of this peak power value. The output was one theta peak frequency value for each participant, which was calculated by averaging over five ROI electrodes (Fz, F8, Pz, P8, Oz). Next, $\Delta\theta$ was computed by subtracting 5 Hz from the aforementioned theta peak frequency value. Hence, for each participant six $\Delta\theta$ values were obtained, i.e., one pre tACS and one post tACS, for in-phase, anti-phase, and sham stimulation. Finally, we assessed the strength of the linear association between $\Delta\theta$ and log-transformed RTs by means of a Pearson correlation (Bonferroni corrected).

# RESULTS

## Behavioral Data

When asked whether stimulation was real or sham, participants were not able to tell reliably [$\chi^2(2) = 5.85$, $p > 0.05$].

Moreover, no differences in RTs between stimulation conditions (in-phase/anti-phase/sham) were found in the motor response task, as evidenced by a one-way RM ANOVA [$F(2,32) = 0.40$, $p > 0.05$]. Hence, a behaviorally facilitating stimulation of the motor cortex can be ruled out.

The 3x3x2 RM ANOVA of log-transformed RTs (assessed during the MtS task) with the within-subject factors TIME, STIMULATION and LOAD showed a main effect for TIME [$F(2,34) = 24.1$, $p < 0.0001$] as well as LOAD [$F(1,17) = 623.1$, $p < 0.0001$], i.e., RTs during the high load condition were larger than during the low load condition. There were no statistically significant effects for STIMULATION or any of the factor interactions (all $ps > 0.05$) (see **Figure 5**). RTs improved over the course of the experimental session (pre-peri-post), i.e., the fastest responses were measured post-stimulation. Importantly, this improvement could be observed across all three stimulation conditions. With respect to accuracy rates, the 3x3x2 RM ANOVA yielded similar results: a main effect for TIME [$F(2,34) = 6.83$, $p < 0.05$] as well as LOAD [$F(1,17) = 87.6$, $p < 0.0001$], and no statistically significant effects for STIMULATION or any of the factor interactions (all $ps > 0.05$) (see **Figure 6**).

## EEG Data

The 2x3x18 RM ANOVA with the within-subject factors PRE_POST, STIMULATION, and ELECTRODE revealed a main effect for ELECTRODE in every analyzed frequency band [delta: $F(3,53) = 8.49$, $p < 0.0001$, theta: $F(3,53) = 8.4$, $p < 0.0001$, alpha: $F(2,26) = 9.33$, $p < 0.05$, beta: $F(3,45) = 17.9$, $p < 0.0001$]. There were no other significant main effects (all $ps > 0.05$). Regarding the PRE_POST × STIMULATION interaction, no frequency band showed significant effects [delta: $F(2,34) = 0.18$, $p > 0.05$; theta: $F(1,23) = 0.54$, $p > 0.05$; alpha: $F(1,23) = 1.6$, $p > 0.05$; beta: $F(1,21) = 0.6$, $p > 0.05$]. Moreover, the analysis did not yield any significant PRE_POST × STIMULATION × ELECTRODE interactions for the delta [$F(34,578) = 0.58$, $p > 0.05$], theta [$F(34,578) = 1.05$, $p > 0.05$], and beta [$F(34,578) = 1.2$, $p > 0.05$] frequency bands. However, in the alpha frequency band, we observed a significant interaction: [$F(34,578) = 1.8$, $p < 0.05$]. **Figure 7** displays power spectrograms of resting EEG for the three stimulation conditions (in-phase, anti-phase, and sham) before and after stimulation.

To further test the effect of stimulation (i.e., stimulation conditions vs. sham) on the alpha peak power, we run two separate ANOVAs (in-phase vs. sham, and anti-phase vs. sham) over five ROI electrodes (Fz, F8, Pz, P8, Oz). When comparing in-phase and sham stimulation conditions, a significant interaction PRE_POST × STIMULATION was found: $F(1,17) = 5.7$, $p < 0.05$. Interestingly, *post hoc* paired samples *t*-tests (with the dependent variable being the mean of the aforementioned ROI electrodes) revealed

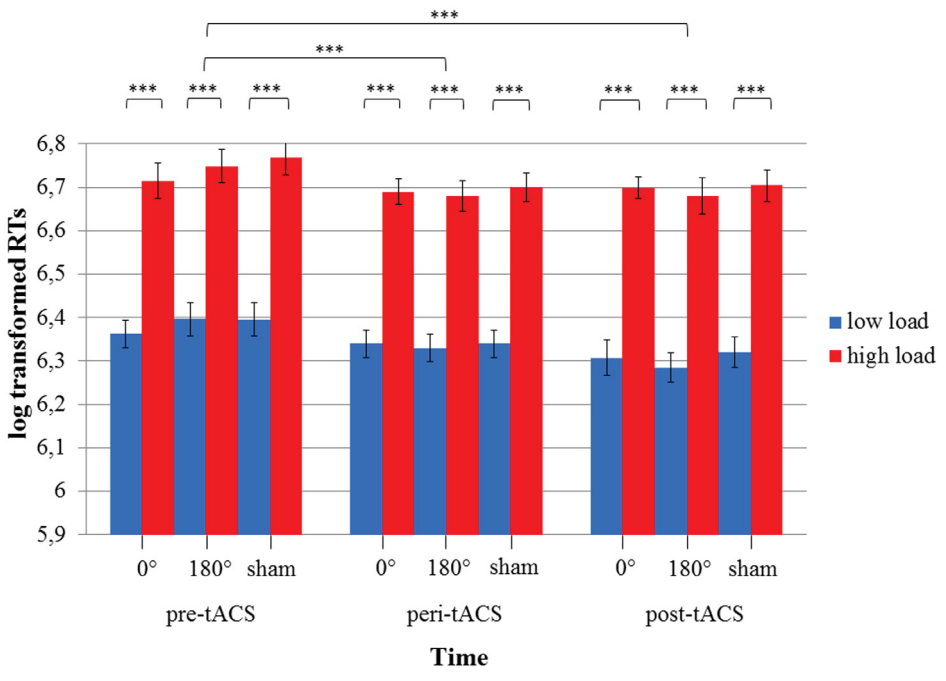


**FIGURE 5 |** Diagram of log-transformed reaction times (RTs) during the visuospatial match-to-sample task. Significant differences between low and high load in each of the three stimulation conditions (0° = in-phase, 180° = anti-phase, and sham) for pre-, peri-, and post-tACS as well as significant differences between pre-, peri-, and post-tACS are shown. (***$p < 0.001$) Standard error bars are displayed.

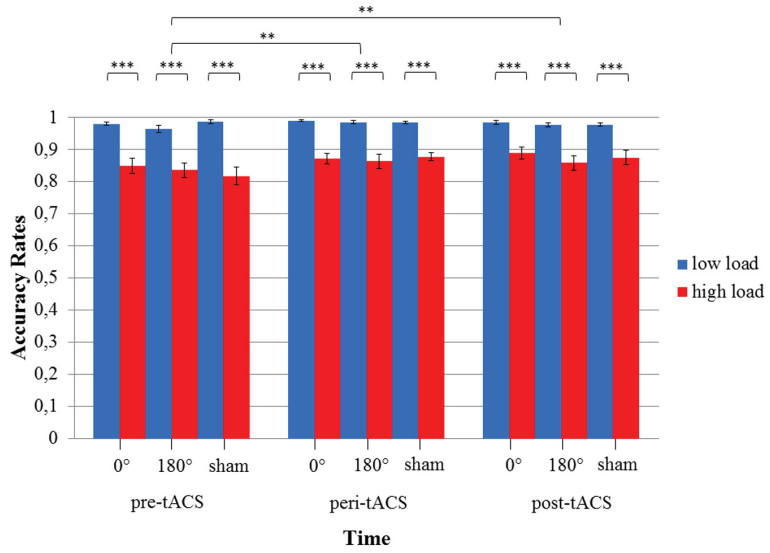


**FIGURE 6 |** Diagram of accuracy rates during the visuospatial match-to-sample task. Significant differences between low and high load in each of the three stimulation conditions (0° = in-phase, 180° = anti-phase, and sham) for pre-, peri-, and post-tACS as well as significant differences between pre-, peri-, and post-tACS are shown. (***$p < 0.001$; **$p < 0.05$) Standard error bars are displayed.

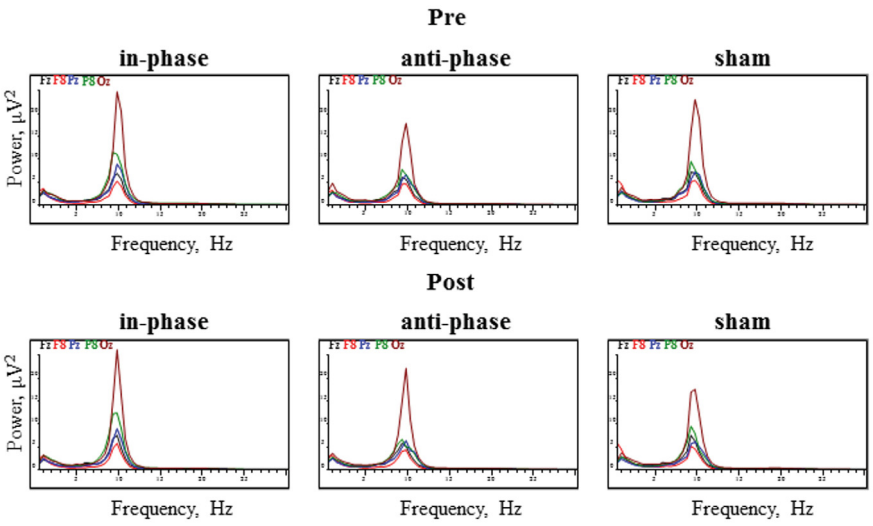


**FIGURE 7 |** Power spectrograms of resting EEG before and after stimulation for the three stimulation conditions (in-phase, anti-phase, and sham). EEG power (in $\mu V^2$) for the five electrodes within direct vicinity of the stimulation sites, i.e., Fz, F8, Pz, P8, and Oz is displayed.

that the pre vs. post contrast was only significant for sham stimulation [$t(17) = 2.2$, $p < 0.05$] but not for in-phase stimulation [$t(17) = -0.09$, $p > 0.05$]. The alpha peak power significantly decreased from pre to post after sham stimulation, whereas it stayed constant for in-phase stimulation. The 2x2x5 RM ANOVA (pre/post, anti-phase/sham, Fz/F8/Pz/P8/Oz) did not yield any statistically significant interactions (all $ps > 0.05$).

Contrary to our experimental hypothesis, there were no significant changes in the EEG power spectrum from pre to post for the stimulation frequency (theta band) (see **Table 2** for details). **Figure 8** illustrates mean peak power values pre

**TABLE 2 |** Mean theta peak power values, standard errors, and confidence intervals for pre/post and stimulation conditions (in-phase/anti-phase/sham).

| | | | | 95% Confidence interval | |
|---|---|---|---|---|---|
| **Condition** | **Stimulation** | **Mean** | ***SE*** | **Lower bound** | **Upper bound** |
| Pre | In-phase | 1.67 | 0.30 | 1.04 | 2.31 |
| | Anti-phase | 1.63 | 0.29 | 1.02 | 2.24 |
| | Sham | 1.90 | 0.39 | 1.08 | 2.71 |
| Post | In-phase | 1.83 | 0.33 | 1.14 | 2.52 |
| | Anti-phase | 1.76 | 0.31 | 1.10 | 2.42 |
| | Sham | 1.83 | 0.36 | 1.08 | 2.58 |

*EEG electrodes in immediate vicinity of stimulation electrodes, i.e., Fz, F8, Pz, P8, Oz were used in order to compute mean peak power values.*

as well as post-stimulation for the delta, theta, alpha, and beta range.

## Correlation Analysis of EEG and Behavioral Data

Markedly, alpha peak power positively correlated with RTs, before as well as after the stimulation (see **Table 3**). This effect was observed in the in-phase and sham conditions, whereas the trend did not reach significance in the anti-phase condition. In other words, the stronger the alpha power, the slower participants responded during the behavioral task. Alpha power values before the task during the resting period could predict performance in the MtS task, as revealed by a bivariate Pearson correlation between log-transformed RTs and alpha peak power before the stimulation (in-phase: $r = 0.52$, $p < 0.05$; anti-phase: $r = 0.4$, $p > 0.05$; sham: $r = 0.55$, $p < 0.05$) (see **Figure 9**).

**TABLE 3 |** Correlations between alpha peak power and log transformed RTs for pre/post and stimulation conditions (in-phase/anti-phase/sham).

| | **Stimulation** | | |
|---|---|---|---|
| **Condition** | **In-phase** | **Anti-phase** | **Sham** |
| Pre | $r = 0.52$, $p = 0.03$ | $r = 0.40$, $p = 0.11$ | $r = 0.55$, $p = 0.02$ |
| Post | $r = 0.52$, $p = 0.03$ | $r = 0.36$, $p = 0.15$ | $r = 0.57$, $p = 0.01$ |

Furthermore, there was a significant positive correlation between $\Delta\theta$ and log transformed RTs, which could only be observed post-stimulation and only in the anti-phase condition (in-phase: $r = 0.27$, $p > 0.05$; anti-phase: $r = 0.6$, $p < 0.05$; sham: $r = -0.13$, $p > 0.05$) (see **Figure 10**). The closer participants' individual theta peak frequency was to the stimulation frequency of 5 Hz, the faster they responded during the behavioral task.

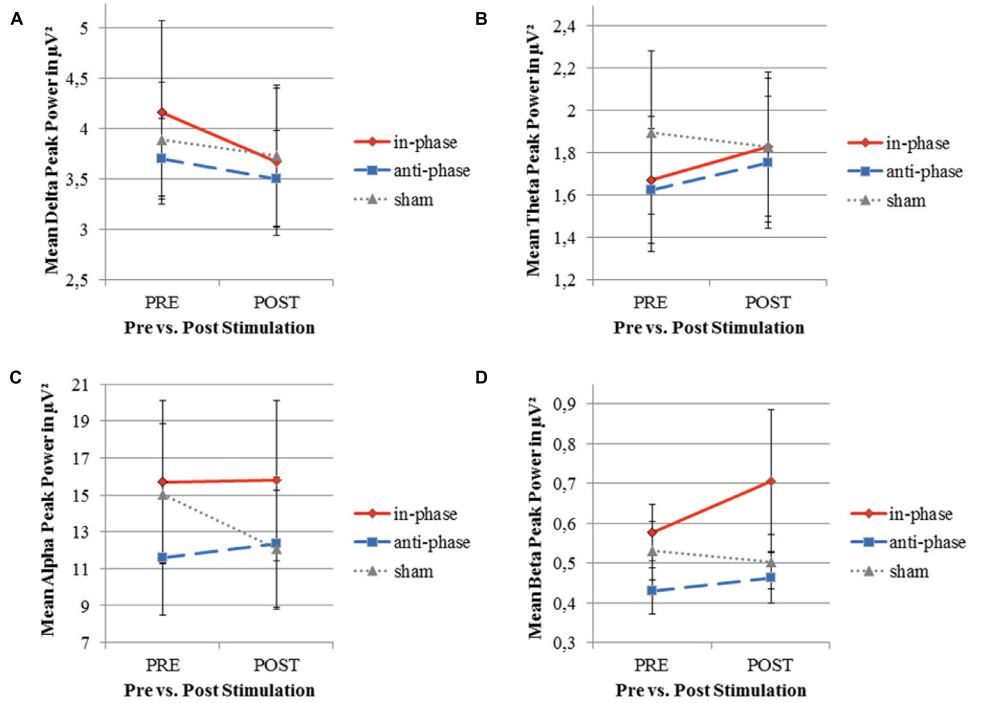


**FIGURE 8 |** Mean peak power of resting EEG (delta, theta, alpha, and beta frequency bands) before and after stimulation for the three stimulation conditions (in-phase, anti-phase, and sham). **(A)** Delta frequency range (0.5-4 Hz). **(B)** Theta frequency range (4-8 Hz). **(C)** Alpha frequency range (8-12 Hz). **(D)** Beta frequency range (12-30 Hz). Peak power (in $\mu V^2$) was averaged across five electrodes within direct vicinity of the stimulation sites, i.e., Fz, F8, Pz, P8, and Oz. Standard error bars are displayed.

On the other hand, $\Delta\theta$ values before stimulation did not significantly correlate with log transformed RTs during the MtS task (in-phase: $r = 0.14$, $p > 0.05$; anti-phase: $r = 0.24$, $p > 0.05$; sham: $r = -0.2$, $p > 0.05$).

# DISCUSSION

## Lack of Frequency-Specific EEG Aftereffects

The present exploratory study did not show any EEG power enhancement for the tACS-targeted theta frequency band. This finding is in line with results recently published by Wischnewski et al. (2016), who did not observe any changes in resting EEG after theta tACS compared to sham. However, these authors reported a significant decrease in theta-beta EEG ratios at frontal recording sites following active tACS.

Our analyses of other frequency bands revealed, nonetheless, a frequency-unspecific effect in the alpha frequency band. We report a significant drop of EEG alpha power in sham, whereas alpha power remained equal from pre to post in the in-phase and anti-phase conditions. EEG power did not differ significantly between anti-phase and in-phase tACS in any frequency band.

With regard to memory processes, Klimesch et al. (2006) stated that resting or reference alpha power was positively related to participants' performance. The results of the present study – log transformed RTs during the task and alpha power before stimulation correlate positively – confirm this finding by Klimesch and colleagues. This suggests that resting alpha power before stimulation is a good predictor of WM performance.

Interestingly, Klimesch and colleagues also observed that event-related alpha desynchronization (ERD), reflected by small power during the actual task, was associated with good performance (Klimesch et al., 2006). Moreover, in an earlier study, Klimesch (1999) has found evidence that the extent of alpha ERD is related to task demands, i.e., as the task becomes more difficult, alpha power drops and theta power increases. Furthermore, the transition between theta synchronization and alpha desynchronization is subject to large inter-individual variability (Klimesch, 1999). Although individual differences with regard to alpha peak frequency strongly depend on age, even for age-matched subjects a considerable inter-individual variability in alpha frequency has been observed (Doppelmayr et al., 1998). Klimesch et al. (1990, 1993) showed that these inter-individual differences in alpha frequency are mainly due to inter-individual differences in memory performance.

Nevertheless, the dissociation between tonic (resting/reference) and phasic (event-related) alpha power provides a tangible explanation for the results of the present experiment. Theta tACS may have increased alpha power on a phasic level in the two active stimulation conditions during the actual WM task, which could have deteriorated participants' behavioral performance, masking the effects of theta power enhancement. The significant decrease in alpha power in the sham condition could be taken as evidence for the alpha desynchronization, crucial for good WM performance.

## Behavioral Findings

The absence of electrophysiological effects in the theta range was paralleled by an absence of behavioral effects between conditions.

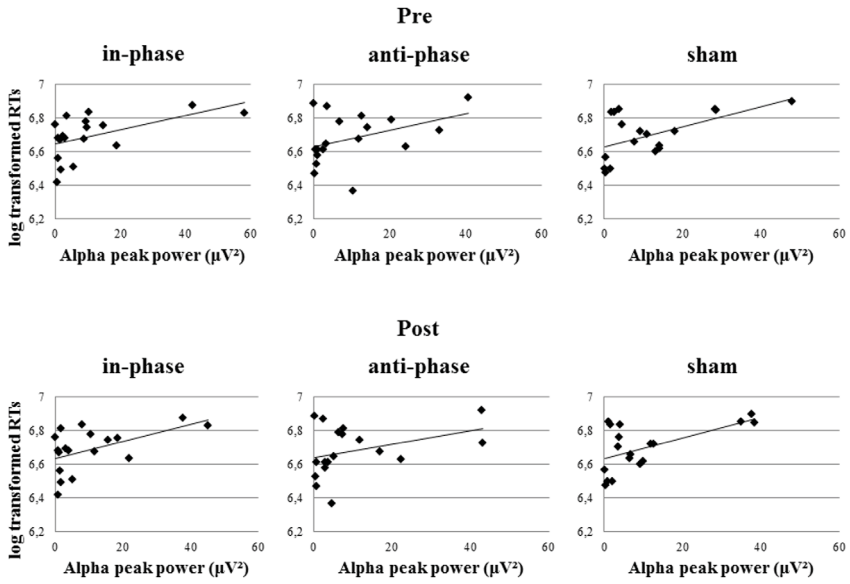


**FIGURE 9 |** Pearson correlations of resting EEG alpha peak power (before and after stimulation) and log transformed RTs during the MtS task during the three stimulation conditions (in-phase, anti-phase, and sham).

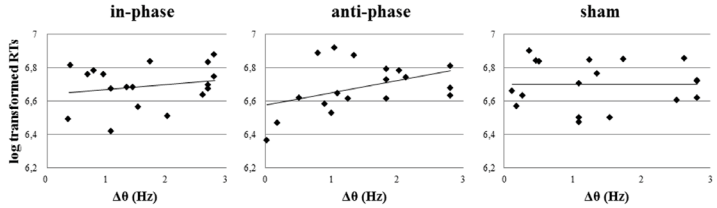


**FIGURE 10 |** Pearson correlations of Δθ post-stimulation and log transformed RTs during the MtS task during the three stimulation conditions (in-phase, anti-phase, and sham).

Contrary to our initial experimental hypotheses, the present study did not show any significant differences in RTs or accuracy rates between the two stimulation conditions (in-phase and anti-phase). Based on these findings, we cannot draw concrete conclusions about the role of theta phase synchronization or desynchronization in WM processes and if tACS can be used to differentiate between in-phase and anti-phase phase-locking between brain areas.

With our analyses we also addressed a possible learning effect. Participants' behavioral performance (RTs and accuracy rates) improved significantly over the course of each experimental session (pre-peri-post). Yet, this behavioral improvement was similar in all stimulation conditions and we can thus rule out a tACS facilitated learning boost.

## Correlation Analysis of EEG and Behavioral Data

Notably, the present study showed that the smaller Δθ in a given subject after anti-phase stimulation, the more behavioral performance during the WM task was facilitated (i.e., faster RTs). This finding is in line with results from Griesmayr et al. (2014) and confirms the correct choice of a 5 Hz target frequency for the specific visuospatial WM paradigm used in the present study. Interestingly, Δθ before stimulation could not predict RTs during the task, but Δθ after stimulation could. The closer a participant's individual theta peak frequency had shifted toward the stimulation frequency after stimulation, the faster her RT during the task. We suggest two possible interpretations for this finding: (A) Frequency shifts were due to entrainment by tACS. (B) Stimulation at individual peak power frequency was not relevant in our experiment, as otherwise Δθ before stimulation should have been a good predictor of RTs. In line with these findings, Helfrich et al. (2014) pointed out that neither baseline power nor the iAPF reliably predicted whether 10 Hz tACS resulted in successful entrainment. Behavioral data by Cecere et al. (2015) further support this interpretation.

## Failed Replication of tACS Phase Manipulation

The present study attempted to replicate the 'synchronization-desynchronization' tACS setup, originally introduced by Polanía et al. (2012). However, three main caveats to this earlier study may underlie the inconsistency of findings between the study by Polanía and colleagues and the present study. First, Polanía and colleagues did not measure participants' EEG, neither before, during nor after the tACS experiment and could thus not provide any direct evidence for enhancement of synchronous brain oscillations in the theta band. Second, electromechanical limitations of the stimulation device used by Polanía and colleagues caused a fundamental methodological problem. Apart from the relative phase angle of stimulation (0 or 180°), the authors could not rule out the possibility that their 'synchronized' group differed in one more important parameter from their 'desynchronized' group, namely amplitude. Due to the specific electrode setup, it is possible that the 'synchronized' group was stimulated with a different intensity than the 'desynchronized' group, which might have caused differences between groups. Recently, Strüber et al. (2013) used a similar protocol successfully with 40 Hz tACS. Nonetheless, they applied two return electrodes in their 'in-phase' condition – one on each hemisphere – and only one return electrode in their 'anti-phase' condition. Since sinusoidal currents constantly switch between active and return electrodes, again, it can be questioned whether the two stimulation conditions used by Strüber and colleagues were comparable after all. Third, a recent review by Thut et al. (2017) raised the issue of the direction of current flow in Polanía and collegues' electrode setup. Whereas the direction of current flow in the 'synchronized' group was F3-Cz/Cz-F3 and P3-Cz/Cz-P3, the direction in the 'desynchronized' group was F3-P3/P3-F3. The present study was specifically designed to overcome these technological limitations. We used a multichannel stimulator with in-house electromechanical adjustments of the stimulation electrodes which enabled us to control for stimulation intensities (i.e., 1 mA peak-to-peak) as well as for the direction of current flow (i.e., F4-Cz/Cz-F4 and P4-Cz/Cz-P4).

## Limitations and Future Directions

With regard to our EEG analyses, a first limitation of the present study lies in the fact that we did not directly take into account inter-individual differences due to following the convention of analyzing fixed frequency bands. Since, on an individual level, theta frequency varies as a function of alpha frequency, this limitation could be overcome in the future by using alpha frequency as a reference point for calculating other frequency bands as suggested by Doppelmayr et al. (1998).

A second limitation is the lack of online-EEG recordings during tACS. Unfortunately, such simultaneous tACS-EEG

recordings are subject to strong artifacts, which impose a substantial drawback to neuroscientific research in the field of non-invasive brain stimulation. Very recently an increasing number of studies have tried to overcome this constraint by implementing complex mathematical algorithms, including principal component analysis (Fehér and Morishima, 2016) or superposition of moving averages (Kohli and Casson, 2015) as well as alternative stimulation paradigms, e.g., sawtooth waves (Dowsett and Herrmann, 2016). Despite these efforts, it has been pointed out by Noury et al. (2016) that physiological processes, such as heartbeat and respiration, modulate stimulation artifacts in a non-linear manner. Hence, until now current techniques have failed to remove artifacts entirely. Nonetheless, the concurrent use of tACS and neuroimaging methods such as MEG (Neuling et al., 2015), EEG (Helfrich et al., 2014) or fMRI (Vosskuhl et al., 2016) and the possibility of source reconstruction and mapping tACS entrained cortical oscillations (Witkowski et al., 2016) might yield crucial insights into the online effects of electrical brain stimulation in the future.

A third limitation of our study lies in the choice of stimulation frequency, i.e., 5 Hz. Even though Polanía et al. (2012) and Griesmayr et al. (2014), for instance, have shown that fronto-parietal theta coupling might constitute a key mechanism in WM processes, phase relationships in other frequency bands have as well been found to play crucial roles. Alpha-band oscillations might not only be linked to inhibition (i.e., attention suppression), but also to the selection of stored information (Klimesch, 2012). Furthermore, Bonnefond and Jensen (2012) reported stronger alpha power increase and phase adjustment within occipito-temporal brain areas prior to anticipated distractors as a possible protective mechanism of WM maintenance. Roux and Uhlhaas (2014) further proposed the idea that rhythmic activity at different frequency bands may reflect functional task-dependent differences in WM processes. On the one hand, the authors advocate the involvement of theta oscillations in the sequential coding of WM items. On the other hand, they highlight the occurrence of alpha activity during visual and/or spatial tasks that depend upon the maintenance of simultaneously presented items. Nonetheless, such a visuospatial task with simultaneous presentation of WM material also revealed fronto-parietal phase synchronization within the beta and gamma frequency bands (Babiloni et al., 2004). Besides, Klimesch et al. (2004) have pointed out that alpha-theta phase locking is associated with semantic and WM performance. Had we thus chosen a different stimulation frequency for the present study, we would have possibly observed different behavioral and electrophysiological effects. In the future, more sophisticated protocols could offer the prospect of multi-frequency stimulation in order to tackle research questions regarding cross-frequency coupling, as suggested by Novembre et al. (2017).

## CONCLUSION

The synchronization of oscillatory phases between distant cortical areas seems to be a fundamental neural mechanism, which has proven to be highly relevant for process binding, large-scale communication and integration of neural networks (Womelsdorf et al., 2007; Siegel et al., 2012). The present exploratory study intended to investigate whether such synchronous oscillations are a mere epiphenomenon or actually serve a causal purpose in WM. TACS is widely considered a valuable method in cognitive neuroscience (Herrmann et al., 2013). However, how tACS precisely entrains neural oscillations is still subject to an ongoing debate (Thut et al., 2011; Underwood, 2016). The results of this study emphasize that the modulation of intrinsic neural oscillations by tACS is not simple and one-dimensional. While tACS has repeatedly been shown to impact neural oscillations in a frequency-specific manner (e.g., Zaehle et al., 2010) with subsequent effects on sensation and behavior (Feurra et al., 2011), the absence of frequency-specific effects on neural oscillations (Brignani et al., 2013; for review see Veniero et al., 2015), as well as the absence of behavioral effects on WM performance have been reported elsewhere (Santarnecchi et al., 2016). With the well-known negative publication bias in mind (Fanelli, 2011; Bikson et al., 2014), the negative results of this study should be seen as a cautionary reminder that the precise mechanisms of how tACS impacts neuronal circuits are still unclear. Recently, much work has targeted these precise mechanisms and effects (Neuling et al., 2012; Datta et al., 2013; for review see Ling et al., 2016; Thut et al., 2017) with the aim to ensure tighter control of experimental set-ups and stimulation parameters (Datta et al., 2009; Bikson et al., 2010; Dmochowski et al., 2011). Once our understanding of tACS accounts, for instance, for both frequency-specific and frequency-unspecific effects, tACS may reach its full potential as an experimental tool to causally test hypotheses on principles of neural oscillations.

## AUTHOR CONTRIBUTIONS

M-LK, VM, and CS designed the study, M-LK acquired and analysed the data. M-LK, VM, and CS discussed the results, and M-LK wrote the article. All authors read and approved the final version of the manuscript.

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## SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: http://journal.frontiersin.org/article/10.3389/fnhum.2017.00367/full#supplementary-material

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# Hyper-Transcranial Alternating Current Stimulation: Experimental Manipulation of Inter-Brain Synchrony

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We walk together, we watch together, we win together: Interpersonally coordinated actions are omnipresent in everyday life, yet the associated neural mechanisms are not well understood. Available evidence suggests that the synchronization of oscillatory activity across brains may provide a mechanism for the temporal alignment of actions between two or more individuals. In an attempt to provide a direct test of this hypothesis, we applied transcranial alternating current stimulation simultaneously to two individuals (hyper-tACS) who were asked to drum in synchrony at a set pace. Thirty-eight female-female dyads performed the dyadic drumming in the course of 3 weeks under three different hyper-tACS stimulation conditions: same-phase-same-frequency; different-phase-different-frequency; sham. Based on available evidence and theoretical considerations, stimulation was applied over right frontal and parietal sites in the theta frequency range. We predicted that same-phase-same-frequency stimulation would improve interpersonal action coordination, expressed as the degree of synchrony in dyadic drumming, relative to the other two conditions. Contrary to expectations, both the same-phase-same-frequency and the different-phase-different-frequency conditions were associated with greater dyadic drumming asynchrony relative to the sham condition. No influence of hyper-tACS on behavioral performance was seen when participants were asked to drum separately in synchrony to a metronome. Individual and dyad preferred drumming tempo was also unaffected by hyper-tACS. We discuss limitations of the present version of the hyper-tACS paradigm, and suggest avenues for future research.

**Keywords: joint action, interpersonal coordination, hyperscanning, tACS**

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## INTRODUCTION

### Inter-Brain Synchronization during Joint Action

Joint actions abound in everyday life. When passing plates at the dinner table, when enjoying card games or when playing music together (Keller et al., 2014), we always need to coordinate our actions with others in time and space (Sebanz et al., 2006). Shared task representations have been suggested as the foundation of coordinated joint action (Knoblich et al., 2011). During

joint action, humans appear to represent not only their own motor actions, but also the actions currently being performed and to be performed by their co-actors (Vesper et al., 2010). For example, cues prompting a co-actor to move activate neural processes associated with mental state attribution and motor inhibition (Ramnani and Miall, 2004; Tsai et al., 2006). Conceptually speaking, multiple persons engaged in a coordinated action may share one or more joint forward models to regulate their actions (Sänger et al., 2011). If interacting dyads predict and monitor the sensory outcomes of both partners' actions and make adjustments based on both action outcomes, one would expect interpersonal coupling dynamics to emerge during joint actions. Indeed, studies comparing *intra*-personal coordination to *inter*personal coordination showed that both cases rely on the same dynamical organizing principles (Schmidt and Richardson, 2008), in the sense that the limbs of two different persons, just as the different limbs of one person, form a coupled unit. Schmidt and Richardson (2008) suggested that the organizing principles predicted by the coordination dynamics approach "can operate in neurally based behavioral oscillatory systems that are coupled by perceptual information and, consequently, that these principles represent a universal self-organizing strategy that occurs at multiple scales of nature."

Recent interaction experiments using EEG-hyperscanning, the simultaneous recording of multiple persons' EEG signals (Babiloni et al., 2007a), suggest that these organizing principles extend to the neural level in the form of inter-brain oscillatory couplings (Sänger et al., 2011; Konvalinka and Roepstorff, 2012). Various forms of interpersonally coordinated actions, such as guitar play (Lindenberger et al., 2009; Sänger et al., 2012), gesturing (Dumas et al., 2010) or romantic kissing (Müller and Lindenberger, 2014), were associated with inter-brain synchronization processes predominantly in frequencies below 20 Hz and between fronto-central and parietal sites. Similarly to studies using EEG-hyperscanning, inter-brain synchronized processes have also been observed using the fMRI- and fNRIS-hyperscanning techniques (for review see Babiloni and Astolfi, 2014). Joint action appears to be consistently characterized by changes in inter-brain coupling dynamics, although few studies have attempted to distinguish neural synchronization processes that reflect shared perceptual input and synchronized motor output from those that reflect the emergence of supra-personal coupling processes (Konvalinka and Roepstorff, 2012). Particularly, it remains unclear if inter-brain dynamics causally contribute to joint action performance or if they merely reflect successful action coordination, given that similarities in perceptual input and motor output of two interacting agents tend to be highest when the agents successfully synchronize their actions (Lindenberger et al., 2009; Dumas et al., 2010). To test the existence of a causal nexus between neural and behavioral between-person coupling phenomena, it is desirable to gain greater experimental control over the degree to which oscillatory activity is synchronized across brains.

## Transcranial Alternating Current Stimulation

Transcranial alternating current stimulation (tACS) seems well suited for this purpose. A growing body of studies has shown that tACS is able to modify cortical excitability and activity as well as behavioral performance in various domains, such as memory, learning, or motor function (Antal and Paulus, 2013; Herrmann et al., 2013). Despite increasing interest in the technique, tACS is still in its beginnings, and its precise working mechanisms are still debated (Reato et al., 2013). Using intracranial recordings in animals, Frohlich and McCormick (2010) demonstrated that an electrical field can entrain neuronal firing. Ozen et al. (2010) added that weak electrical currents can also penetrate skull bones and entrain neuronal firing. Though these data suggest that tACS effects may reflect neural entrainment (Herrmann et al., 2013), the precise operation of tACS remains unclear (Thut et al., 2017) and further the efficiency of tACS remains under strong debate (Horvath et al., 2015; Kleinert et al., 2017). Hence the results of the present study need to be interpreted in the context of these ambiguities.

Overall, there is consensus in the literature that tACS affects local and possibly remote oscillatory activity. Applying tACS at frequencies in the EEG range entrains neuronal networks at the applied frequency (Antal and Paulus, 2013; Herrmann et al., 2013), although Kanai et al. (2008) suggested that frequency dependency of tACS is caused by interactions with ongoing oscillatory activity in the stimulated cortex. The capacity of tACS to increase endogenous brain oscillations at the stimulated frequency has been demonstrated in a study for alpha oscillations (Zaehle et al., 2010). TACS applied at alpha and high gamma frequencies over the somatosensory cortex elicits tactile sensations in a frequency-dependent manner (Feurra et al., 2011). Furthermore, such targeting of specific EEG frequency ranges has been shown to enhance performance in the associated cognitive domains. For example, tACS in the alpha range over visual cortex improved performance in a visual conjunction search (Muller et al., 2015). Notably, Polania et al. (2012) demonstrated that 6 Hz tACS applied in-phase at frontal and parietal sites boosted reaction times in a working memory task, while 180° out-of-phase 6 Hz tACS did not. This study provided proof of concept that tACS can be used to modulate intra-brain synchronized networks and the differences between in- and out-of-phase tACS modulation can impact behavior.

## Hyper-tACS as a Means to Manipulate Inter-Brain Synchronization

In the present study, we adapted the logic of the Polania et al. (2012) study to inter-brain synchronized networks. Instead of modulating the oscillatory phase between stimulation electrodes on one head and thus boosting or disrupting intra-brain synchronized oscillations, we applied tACS simultaneously to two individuals (hyper-tACS) to modulate frequency and phase between stimulation electrodes on two heads. In this manner, we hoped to boost or disrupt inter-brain synchronized oscillations, and examine the effect of this manipulation on the degree of behavioral synchronization. We hypothesized that

if inter-brain oscillatory couplings are indeed constitutive for joint action, experimental modulation of inter-brain oscillatory synchronization would affect the degree of interpersonal action coordination.

In order to exert a high degree of experimental control while maintaining the ecological validity and continuous interaction of musical performance paradigms (Acquadro et al., 2016), we used a dyadic drumming paradigm previously established in our lab (Kleinspehn-Ammerlahn et al., 2011). The paradigm was originally derived from the tapping paradigm that has been widely used in the literature to study individual [for review see (Repp, 2005; Repp and Su, 2013)] and more recently also dyadic sensorimotor synchronization abilities (Konvalinka et al., 2010; Vesper and Richardson, 2014). In the classic tapping paradigm, subjects are instructed to tap with their index finger in synchrony with a metronome. Synchronization accuracy is measured as the temporal distance between the finger tap and the metronome click. In dyadic tapping, dyads are instructed to tap symmetrically in synchrony with each other (Konvalinka et al., 2010). One advantage of drumming over tapping is the relatively weaker importance of physical constraints (e.g., finger length) and differences in fine motor skills. Informed by the literature and by the findings in our previous EEG-hyperscanning studies during joint action, we decided to apply tACS at fronto-parietal sites in the theta frequency range over the right hemisphere to target higher-order prediction processes rather than motor processes.

Very recently, Novembre et al. (2017) followed the same logic presented here and applied hyper-tACS during a dyadic finger tapping task. The authors targeted left centroparietal areas at beta frequency to interfere with synchronization processes in motor regions specifically and indeed report facilitation of early inter-personal action synchronization in a same-phase-same-frequency relative to different-phase-same-frequency.

However, inter-brain coupling at *right* centroparietal sites with a topography similar to neuroanatomical sources within the human mirror neuron system (Tognoli et al., 2007) has been observed repeatedly (Tognoli et al., 2007; Dumas et al., 2010) during interpersonal action coordination. This right-lateralized, centroparietal coupling in the alpha-mu range (8–12 Hz), the so-called 'phi complex,' has been put forward as a 'neuromarker for human social coordination' (Tognoli et al., 2007). Notably, the phi complex has been repeatedly observed during an imitation paradigm that involved moving the left as well as the right hand. Thus, the lateralization of the phi complex to the right hemisphere appears independent of motor behavior and instead might reflect the lateralization of mechanism that support coordinated behavior. Specifically, the phi complex has been proposed to reflect 'the influence of the other on a person's ongoing behavior' (Tognoli et al., 2007, p. 8190). Other authors associated oscillations in right centroparietal areas in a broader frequency range (5–15 Hz)[1] with self-other integration (Novembre et al., 2016). Within the context of our paradigm it is of interest that rehearsal mechanisms of rhythmic patterns have been suggested to also reside in the right hemisphere (Riecker et al., 2002). Studies in our own lab showed strongest inter-brain synchronization at frontocentral and centroparietal regions predominantly in the delta and theta ranges during joint guitar play (Lindenberger et al., 2009; Sänger et al., 2012; Müller and Lindenberger, 2014). Strongest inter-brain synchronization effects in the theta range for centroparietal and frontocentral connections have also been reported for cooperation in the prisoner's dilemma (Astolfi et al., 2011). Hence, for the present exploratory study, we chose to integrate these various findings from the literature and opted for a stimulation setup similar to the one previously used by Polania et al. (2012).

[1]Novembre et al. (2016) defined the alpha range for each participant individually as individual alpha peak power (range: 7–13 Hz) ± 2 Hz.

## Contribution and Hypotheses of the Study

In this study we applied hyper-tACS during dyadic drumming to manipulate ongoing inter-brain synchronization to study the effect of this manipulation on interpersonal action synchronization. We hypothesized that if inter-brain oscillatory couplings are indeed constitutive for joint action, experimental modulation of inter-brain oscillatory synchronization would affect the degree of interpersonal action coordination.

In particular, we hypothesized that same-phase-same-frequency hyper-tACS would improve dyadic drumming synchronization, while different-phase-different-frequency hyper-tACS would harm dyadic drumming synchronization. Moreover, we also expected that hyper-tACS would not affect behavioral performance when synchronizing to a metronome, as our stimulation did not target motor processes in the left hemisphere, but coordination processes assumed to reside in the right hemisphere. We furthermore included metronome frequencies harmonic to the stimulation frequencies to control for any potential purely motor impact of the tACS on drumming performance at corresponding harmonic frequencies.

# MATERIALS AND METHODS

## Participants

Initially, 44 female–female dyads participated in the study. Six of the 44 dyads discontinued the experiment, for reasons unrelated to drumming or synchronization performance. Thus, the effective sample consisted of 38 female–female dyads (age range: 20–30 years, mean = 24 years, standard deviation = 2.8 years). Participants did not know each other prior to the study. We decided to include only female participants to prevent effects due to differences in the sex composition of the dyads (Schmid Mast, 2004), as gender distribution in dyads has been found to substantially influence interbrain connectivity patterns (Baker et al., 2016). All participants were right-handed and had normal hearing, full functional mobility in both hands, and no prior musical training. None of the participants suffered from any neurological or psychological disorder, or took medication regularly or during the time the experiment was conducted. Additionally, all of the participants were blind to the hypotheses and conditions of the study.

All participants volunteered for the experiment and gave written informed consent prior to their inclusion in the study. The Ethics Committee of the German Psychology Society approved the study. The study was performed in accordance with the ethical standards laid down in the 1964 Declaration of Helsinki.

## Experimental Setup

Participant pairs were seated back-to-back in an electromagnetically shielded cabin with a portable wall separating both participants. This setup was used to exclude non-verbal communication cues and to allow a relatively tight control of interaction parameters, as the entire flow of information within the dyad was contained in the temporal distribution of the drum beats. Both participants drummed with the drumsticks in their right hands. Drum beats were digitized (Roland drum computer, Germany), and along with auditory instructions and metronome beats (both sent from Intel Xeon, 3.7 GHz PC running Windows 7) played to participants through in-ear headphones, covered by additional soundproof headphones. Drum beat data was recorded from two redundant sources. First, sensors (BIOVISION; single axis, sensitivity: 50 g) attached to the top end of the drumsticks recorded drumstick acceleration, and a peak detection algorithm was used to determine at which exact time points (in milliseconds) drum beats occurred. Second, the digitized drum beat signals were recorded directly via an ExG bipolar amplifier (Brain Products, Munich, Germany) on a second PC (Intel Core i5, 3.2 GHz running Windows XP). Due to technical problems with the acceleration sensors and the higher accuracy of the auditory signal, only the drum beat time series derived from the digitized drum beats were used for further analyses. TACS electrodes were placed first and EEG-electrodes were placed on all sites of a 32-electrodes setup according to the international 10–20 system that were not covered by the tACS electrodes. EEG was thus recorded from both participants with active 21 Ag/AgCl electrodes per person, with the reference electrode at the right mastoid (actiCAP, Brain Products, Munich, Germany). EEG data were collected for a different study, for the present report no EEG data have been analyzed as removal of the tACS-induced EEG-artifact is non-trival.

## Dyadic Drumming Paradigm

The dyadic drumming paradigm used in this study (see **Figure 1**) has been previously established in our lab (Kleinspehn-Ammerlahn et al., 2011). The study comprised three different behavioral conditions (dyadic, metronome, and individual drumming), which were delivered in a pseudorandom trial order. Participants were instructed to hold the drumming frequency stable within any given trial. For individual trials each participant was asked to drum at a freely chosen frequency and participants only heard their own drumbeats. *Individual* was chosen to assess each participant's preferred drumming tempo. For *metronome* trials, participants were asked to drum as precisely as possible in synchrony with a metronome. The metronome beat was varied in a pseudorandom order within and between participants at 1.25, 1.5, or 1.75 Hz. Participants heard both their own drumbeats and the metronome beats. This condition was used to assess each participant's general synchronization ability. For *dyadic*, participants were asked to drum as precisely as possible in synchrony with each other. Participants heard their own and their partner's drumbeats. This condition was used to assess mutual synchronization within the dyad and each dyad's preferred tempo.

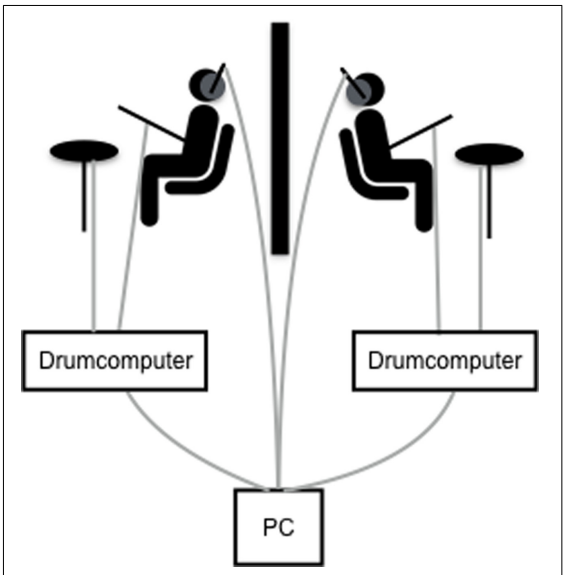


**FIGURE 1 |** Experimental set-up of the dyadic drumming paradigm. Participants sat back-to-back, were separated by a portable wall and drummed in symmetrical synchrony with each other or with a metronome while receiving hyper-tACS. Drum beats were digitized via the drum computer and along with auditory instructions and metronome beats sent from the PC to the participants' headphones. Acceleration sensors were placed on the drum sticks. Cable connections depicted in gray.

All instructions and drum/metronome beats were delivered through headphones. Each trial was prefaced with a word that indicated the condition of the following trial ('joint'/'metronome'/'individual'), followed by a beep that signaled the trial start. After 16 s trial duration, the trial end was signaled by another beep. Subsequently, participants replied to the post-trial questions by button presses. There was one post-trial question for both non-dyadic conditions 'How stable was the frequency of drumming?' for individual trials (1 = bad, 2 = ok, 3 = good) and 'How well did the synchronization go?' for metronome trials (1 = bad, 2 = ok, 3 = good). After dyadic trials, participants answered two questions: 'How well did the synchronization go?' (1 = bad, 2 = ok, 3 = good) and 'Who determined the frequency of drumming?' (1 = me, 2 = both 3 = other).

To assess the influence of hyper-tACS on dyadic, metronome and individual drumming we conducted a multiple-session

study. Each dyad visited the lab for three experimental sessions, separated by 1 week each. Experimental sessions differed only in hyper-tACS parameter and each session consisted of three segments: pre-stimulation (pre), hyper-tACS stimulation (stimulation), and post-stimulation (post). The pre and post segments were identical and consisted of 21 trials each (five individual, eight dyadic, eight metronome; dyadic and metronome trials alternated in blocks of four trials). To maximize dyadic drumming trials during the stimulation segment, this segment consisted of 45 trials (seven individual, thirty dyadic, and eight metronome; blocks of three dyadic trials were separated by one individual/metronome trial in a pseudorandomized order). Session length varied slightly depending on each dyad's speed of answering the post-trial questions. Pre and post lasted 10–12 min each and stimulation lasted 21–25 min (variance is due to dyad's differential response speed to post-trial questions). Participants took a short break between pre and stimulation and between stimulation and post.

## Measures of Behavioral Performance

We used a measure of dyadic drumming asynchrony previously established in our lab, referred to as 'asynchrony score' (for details, see Kleinspehn-Ammerlahn et al., 2011, and Supplementary Material). The measure compares synchrony mismatch between two time series of drumbeats. 'Dyadic asynchrony scores' were computed by calculating the distance between the series of both participants' drumbeats as costs of transforming one series into the other to reach perfect synchrony, and 'metronome asynchrony scores' by analogously comparing one participant's drum beat time series with the corresponding metronome beat time series. The transformation was achieved by either shifting drumbeats to later or earlier points in time or by inserting or deleting drumbeats. Using dynamic programming and by pairing drumbeats in a way that an optimal trade-off between shifting and inserting missing drumbeats was assumed, the algorithm automatically minimized the cost function. Transfer costs are expressed in milliseconds and indicate the duration of the needed time shifts and the additional costs for insertion or deletion of drumbeats, which corresponded to half the mean drumbeat interval of the series in question (see Kleinspehn-Ammerlahn et al., 2011 for a formal description of the asynchrony score algorithm). The measure was chosen for its methodological advantages over more traditional metrics, most importantly its independence from speed changes and its ability to match corresponding taps. The measure has a minimum score of zero at perfect synchrony. Asynchrony sum scores were calculated for each trial. To approximate a normal distribution outliers were removed (>2.5 standard deviation) and asynchrony scores were Lambert-transformed using *R* (R Development Core Team, 2008) and the 'LambertW' package (Goerg, 2011). Preferred drumming tempo was measured as mean inter-response interval in ms for each trial and also Lambert-transformed to approximate a normal distribution. The Lambert-transformed dyadic asynchrony scores, metronome asynchrony scores and individual and dyad preferred tempo served as the dependent variables in this study.

## Hyper-tACS Protocols

Electrical stimulation was delivered through a four-channel direct current stimulator (DC-Stimulator MC; NeuroConn GmbH, Ilmenau, Germany). The tACS stimulator was connected to three conductive rubber electrodes (each 5 cm × 5 cm). Similar to the setup used by Polania et al., 2012[2], on each subject's right hemisphere two stimulation electrodes were placed on F4 (fronto-central) and P4 (parieto-central) of the international 10–20 system. As a multichannel stimulator system was used, each stimulation electrode was connected to one independent channel and both cables of these corresponding return channels were electromechanically soldered into one single merged cable for the return electrode, which was placed on Cz (central). Analog to the protocol used by Polania et al. (2012) stimulation intensity was set to 1mA (peak to peak). The stimulation was automatically ended after 25 min to remain with the range considered safe for use of tACS (see e.g., Antal and Paulus, 2013). In order to apply tACS without irritating the skin under the electrodes, impedance between the electrodes was kept below 20 kOhm throughout the experiment. This was obtained by applying Ten20 conductive gel on the rubber electrodes and onto the hair and skin on the scalp. Also, in order to minimize the sensation caused by sudden stimulus onset, the stimulation intensity was ramped up to the maximum intensity of 1 mA over 30 s and ramped off to zero for 30 s after the stimulation. The sensation on the scalp faded over the initial 1st minute presumably due to adaptation of the skin and the decrease of the impedance. Three different stimulation parameters were used for each dyad in a pseudo-randomized cross-over design (see **Table 1**) that enabled us to control for training effects across sessions. All stimulations were alternating current sinusoidal stimulation within the theta range: (a) 'same-phase-same-frequency stimulation': both subjects received stimulation at 6 Hz with a zero phase difference; (b) 'different-phase-different-frequency stimulation': one subject received 5 Hz

[2]The setup by Polania et al. (2012) has been criticized (Thut et al., 2017) for potentially inducing differences in current flow between the synchronized and desynchronized conditions. In our setup the participant's two 'active' stimulation electrodes were always in-phase and out-of-phase only with respect to the other participant's stimulation electrodes; thus this limitation did not apply to our setup.

**TABLE 1 |** Organization of different stimulation types across sessions.

| Group | Session 1 | Session 2 | Session 3 |
|---|---|---|---|
| A (13 dyads) | Different | Sham | Same |
| B (13 dyads) | Same | Different | Sham |
| C (12 dyads) | Sham | Same | Different |

*The different stimulation conditions were pseudo-randomized across the three experimental sessions in a cross-over design [same-phase-same-frequency: tACS with 6 Hz on both subjects; different-phase-different-frequency: tACS with 5 Hz on one and 7 Hz on the other subject; sham: 6 Hz sham tACS]. Stimulation types: different, different-phase-different-frequency stimulation; same, same-phase-same-frequency stimulation; sham, sham stimulation.*

with 13 degrees offset, the other 7 Hz with 1 degree offset; (c) 'sham stimulation': both subjects received 30 s fade-in and 30 s fade-out of 6 Hz stimulation (Polania et al., 2012). We selected these frequencies so that both stimulation types remained within the theta range, while at the same time the different-frequencies-stimulation used two prime numbers (5 and 7) as the stimulation frequencies so that one stimulation frequency was not a multiple of the other. Current intensity and the frequencies used in this study were chosen to be unlikely to induce perception of phosphenes usually induced by higher frequencies (Kanai et al., 2008). After each stimulation session, subjects filled out a tACS post-questionnaire (Poreisz et al., 2007), which confirmed the absence of phosphenes in this study. Furthermore, none of the subjects experienced lasting discomfort throughout the experiment.

## Statistical Procedures

We used (R Development Core Team, 2008) and *lme4* (Bates et al., 2015) to perform a linear mixed effects analysis of the relationship between behavioral drumming performance and stimulation type. We constructed four separate models with (a) dyadic asynchrony, (b) metronome asynchrony, (c) individual preferred tempo, and (d) dyad preferred tempo as dependent variables. As fixed effects, we entered condition (1:7), which was a combination of stimulation type (sham; same-phase-same-frequency; different-phase-different-frequency) and experimental segment (pre-stimulation, stimulation, post-stimulation): (1) pre-stimulation, (2) sham stimulation, (3) same-phase-same-frequency stimulation, (4) different-phase-different-frequency stimulation, (5) sham post-stimulation, (6) same-phase-same-frequency post-stimulation, and (7) different-phase-different-frequency post-stimulation. Dyad-level intercepts and by-dyad slopes of drumming exposure in weeks were considered random effects [behavioral performance ∼ condition (1+ drumming exposure in weeks| dyad)]. We used *MASS* (Venables and Ripley, 2002) to create customized contrast matrices to directly compare conditions of interest.

Visual inspection of residual plots did not reveal any obvious deviations from homoscedasticity or normality. *P*-values for the effect of condition were obtained by likelihood ratio tests of the full model with the effect in question [behavioral performance ∼ condition (1+ drumming exposure in weeks| dyad)] against the model without the effect in question [behavioral performance ∼ (1+ experimental session| dyad)]. *P*-values for all individual factor levels of the fixed effects were calculated from *F* statistics of types I–III hypotheses using Satterthwaite's approximation for denominator degrees of freedom. The tests on random effects were performed using likelihood ratio tests (both implemented in *R* statistical software using 'lmerTest'). We further used a series of Welch's unequal variance *t*-tests to analyze mean differences between individual and preferred tempo and an *F*-test to analyze differences in variance. To specifically test the relationship between individual preferred tempo and dyad preferred tempo we performed another linear mixed effects analysis. The dependent variable was dyad preferred tempo, as fixed effects we entered individual A preferred tempo and individual B preferred tempo, random effects were again intercepts for dyads and by-dyad random slopes for the effect of week.

# RESULTS

## Dyadic Asynchrony

Linear mixed model analysis showed differential effects for conditions (combination of stimulation type and experimental segment) on dyadic asynchrony [$\chi^2(6) = 60.21$, $p < 0.001$]. Relative to pre-stimulation, same-phase-same-frequency stimulation and different-phase-different-frequency stimulation did not change dyadic asynchrony [$t(4856) = 0.872$, $p = 0.383$; $t(4868) = -1.444$, $p = 0.149$], while dyadic asynchrony decreased for sham stimulation and all post-stimulation conditions (all $p < 0.05$, see **Figures 2**, **3**). We estimated the regression model with customized contrast matrices to compare sham stimulation to the mean of same-phase-same-frequency stimulation and different-phase-different-frequency stimulation. Relative to sham stimulation, dyadic asynchrony increased under active stimulation [$\beta = 84.72$, $SE = 21.89$, $t(4499) = 3.870$, $p < 0.0005$]. Relative to same-phase-same-frequency stimulation, different-phase-different-frequency stimulation decreased dyadic asynchrony [$\beta = -49.50$, $SE = 24.14$, $t(4791) = -2.050$, $p < 0.05$]. Relative to sham post-stimulation the mean dyadic asynchrony across different-phase-different-frequency post-stimulation and same-phase-same-frequency post-stimulation was increased [$\beta = 78.63$, $SE = 34.34$, $t(4890) = 2.290$, $p < 0.05$]. We observed no difference when comparing different-phase-different-frequency post-stimulation directly to same-phase-same-frequency post-stimulation [$t(5904) = 0.419$, $p = 0.675$]. Random effects accounted for 72.30% of variance in dyadic asynchrony scores.

## Metronome Asynchrony

Linear mixed model analysis showed differential effects for conditions (combination of stimulation type and experimental segment) on metronome asynchrony [$\chi^2(6) = 146.65$, $p < 0.001$]. Relative to pre-stimulation, metronome asynchrony was increased in all three stimulation conditions, but in no post-stimulation condition (all $p > 0.05$, see **Figures 2**, **3**). In analogy to the analysis of dyad asynchrony we used customized contrast matrices to compare sham and active tACS conditions directly. Metronome asynchrony during same-phase-same-frequency stimulation did not differ from metronome asynchrony during different-phase-different-frequency stimulation [$t(4830) = 1.434$, $p = 0.152$]. Further, metronome asynchrony during sham stimulation was not different from mean metronome asynchrony across same-phase-same-frequency stimulation and different-phase-different-frequency stimulation [$t(4607) = 0.474$, $p = 0.636$]. Same-phase-same-phase-same-frequency post-stimulation was not different from different-phase-different-frequency post-stimulation [$t(4730) = 0.436$, $p = 0.663$], neither was metronome asynchrony during sham post-stimulation different from mean metronome asynchrony across same-phase-same-frequency

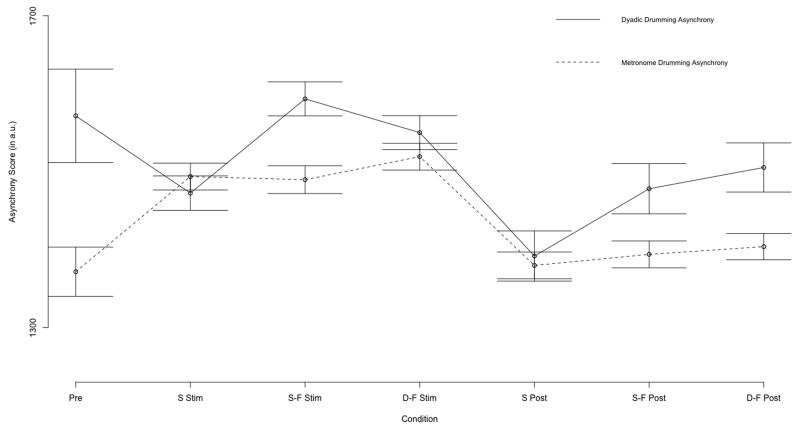


**FIGURE 2 |** Results of the fixed effect of the linear mixed model analysis for the effect of condition on dyadic and metronome asynchrony scores. Displayed are mean asynchrony scores as estimated by the model. Stimulation conditions: Pre, pre; S Stim, sham stimulation; S-F Stim, same-phase-same-frequency stimulation; D-F Stim, different-phase-different-frequency stimulation; S Post, sham post; S-F Post, same-phase-same-frequency post; D-F Post, different-phase-different-frequency post. Standard errors are indicated by horizontal lines.

post-stimulation and different-phase-different-frequency post-stimulation [$t(4570) = 0.835$, $p = 0.404$]. The random effects accounted for 48.92% of total variance in metronome asynchrony. Whether or not the metronome frequency was harmonic to the stimulation frequency did not effect metronome asynchrony score. A mixed model with metronome frequency, stimulation frequency and harmonic (as a factor) did not perform better than a model containing only the random effects subject id and weeks of drumming exposure [$\chi^2(3) = 0.205$, $p = 0.977$].

## Direct Comparison of Dyadic and Metronome Asynchronies

**Figure 2** illustrates mean metronome asynchrony scores for all experimental conditions. A direct comparison between dyadic asynchrony and metronome asynchrony for sham tACS revealed a striking similarity between metronome asynchrony scores and dyadic asynchrony scores (see **Figure 4**). For sham tACS, participants were better at synchronizing with a metronome only at the beginning of the experiment (pre-stimulation) [Welch's unequal variance $t$-test: $t(1253) = 10.528$, $p < 0.001$], while they performed just as well in dyadic drumming during the experimental segments stimulation [$t(1536) = -0.139$, $p = 0.89$] and post-stimulation [$t(467) = 0.569$, $p = 0.570$]. Overall, dyads improved in dyadic synchronization over the course of the experimental session (pre-stimulation > stimulation > post-stimulation), while participants' synchronization to the metronome was best during pre-stimulation (see **Figures 2**, **4**). The linear mixed model analyses showed a differential impact of tACS on metronome asynchrony scores vs. dyadic asynchrony scores. **Figure 4** visualizes the impact of sham tACS and the two active stimulation protocols onto dyadic asynchrony vs. metronome asynchrony: mean metronome asynchrony scores [averaged across all three experimental segments (pre-stimulation, stimulation, post-stimulation)] and mean dyadic asynchrony scores were similar for sham tACS. Only mean metronome asynchrony scores remained stable for the two active stimulation protocols, while mean dyadic asynchrony scores were increased for both active stimulation protocols.

## Individual Preferred Tempo

Mean individual preferred inter-tap interval across all experimental segments and sessions was 593.21 ms ($SE = 237.31$ ms) and did not differ from the mean across sham trials [$M = 591.05$ ms, $SE = 230.83$ ms, Welch's unequal variance $t$-test: $t(678) = 0.200$, $p = 0.841$]. However, individual preferred tempo for pre-stimulation trials was different from the tempo across all preferred tempo trials [$M = 637.64$ ms, $SE = 255.55$ ms, Welch's unequal variance $t$-test: $t(1779) = -5.261$, $p < 0.0001$]. Linear mixed model analysis showed differential effects for conditions (combination of stimulation type and experimental segment) on individual preferred tempo [$\chi^2(6) = 118.54$, $p < 0.0001$, see **Figures 5**, **6**]. Relative to pre-stimulation, individual preferred inter-tap interval was decreased in all other conditions (all $t > 3.488$, $p < 0.0001$). Customized contrasts showed no difference in individual preferred tempo between same-phase-same-frequency stimulation and different-phase-different-frequency stimulation [$t(2854) = -01.618$, $p = 0.105$], nor a difference in individual preferred tempo between sham stimulation and the mean across both active tACS stimulations [$t(2571) = -0.656$, $p = 0.512$].

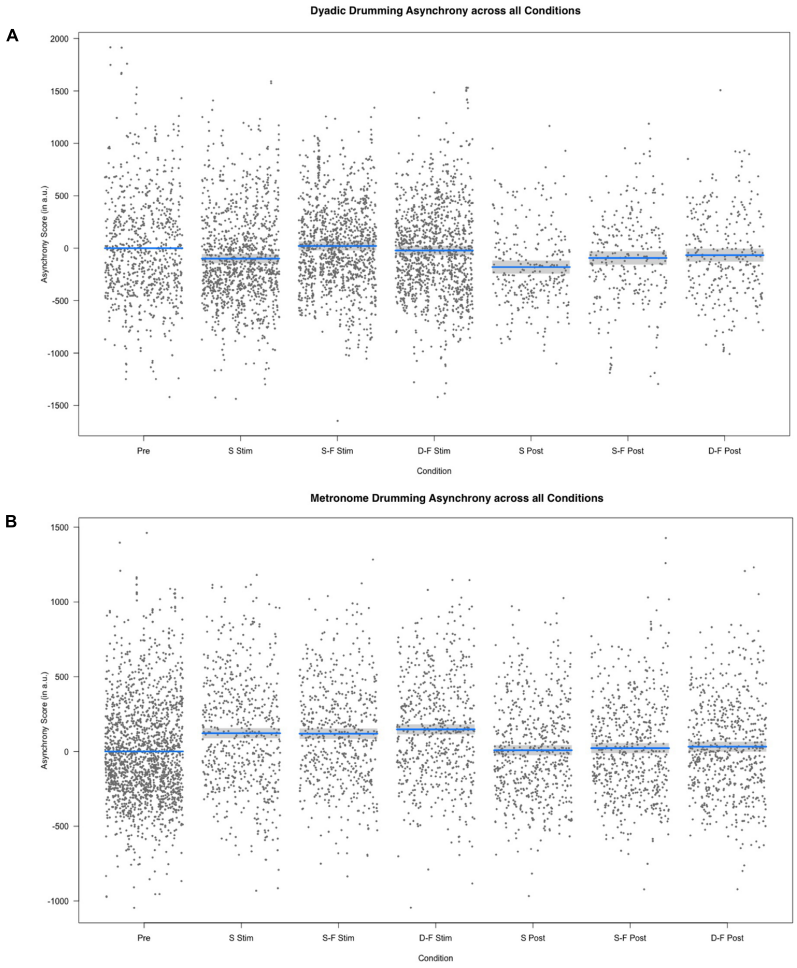


**FIGURE 3 |** Results of the fixed effect of the linear mixed model analysis for the effect of condition on asynchrony scores. **(A)** Partial residuals as estimated by the mixed model for dyadic drumming. **(B)** Partial residuals as estimated by the mixed model for metronome drumming. Stimulation conditions: Pre, pre; S Stim, sham stimulation; S-F Stim, same-phase-same-frequency stimulation; D-F Stim, different-phase-different-frequency stimulation; S Post, sham post; S-F Post, same-phase-same-frequency post; D-F Post, different-phase-different-frequency post. Blue lines indicate model prediction values. 95% confidence intervals are displayed as gray bands.

Preferred tempo also did not differ between same-phase-same-frequency and different-phase-different-frequency post-stimulation [$t(3295) = -0.399$, $p = 0.690$], neither differed it between sham post-stimulation and the mean across same-phase-same-frequency and different-phase-different-frequency post-stimulation [$t(3104) = -1.371$, $p = 0.170$]. The random effects explained 44.87% variance in preferred tempo.

## Dyadic Preferred Tempo

Mean dyad preferred inter-tap interval across all experimental segments and sessions was 515.06 ms ($s = 138.99$ ms) and it was not different from mean across sham trials alone [$M = 511.57$ ms, $s = 121.34$ ms; Welch's unequal variance $t$-test: $t(1695) = 0.826$, $p = 0.409$]. We tested the difference between overall individual preferred tempo and overall dyadic preferred tempo with a Welch's unequal variance $t$-test [$t(5887) = -18.192$, $p < 0.0001$]. This difference was also significant when comparing individual and preferred tempo only on trials before any stimulation was applied (pre-stimulation) [$t(1913) = -9.164$, $p < 0.0001$] or when comparing only sham trials [$t(667) = -7.378$, $p < 0.0001$]. Furthermore, variance (Var) was higher for individual preferred tempo than for dyad preferred tempo [Var (individual) = 56317.64, Var (dyad) = 19318.06; $F(4955) = 0.343$, $p < 0.0001$]. See

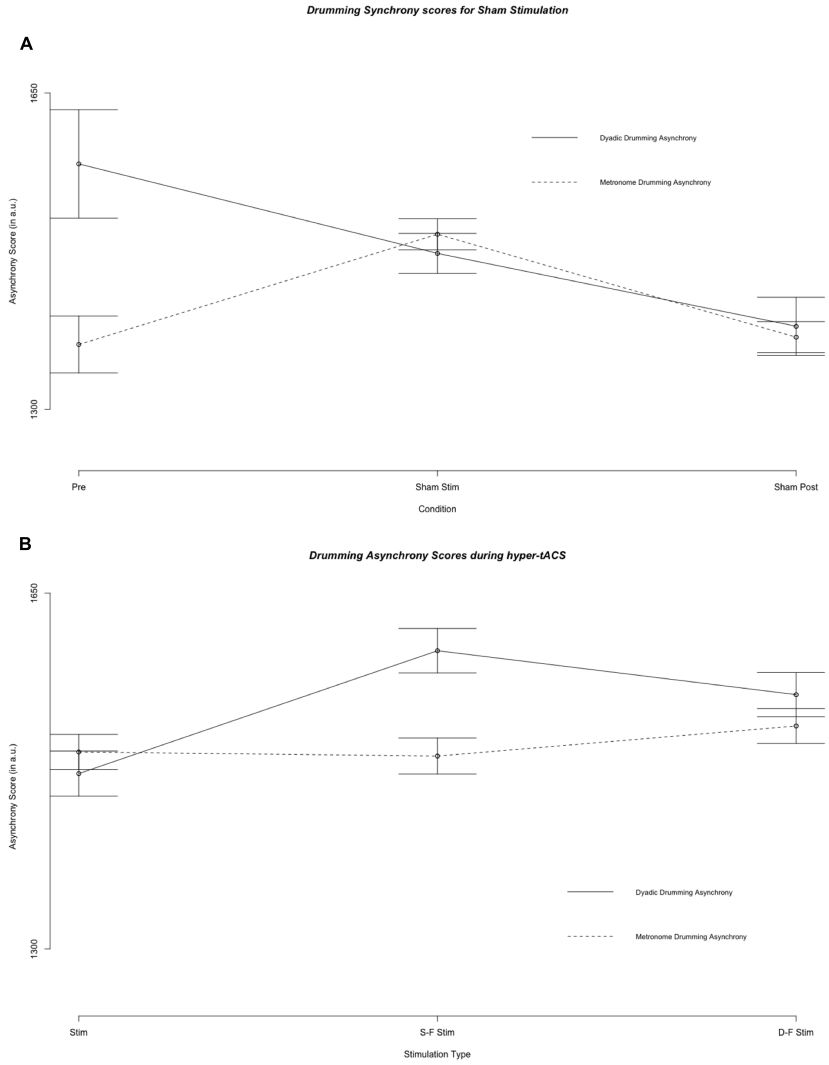


**FIGURE 4 |** Results of the fixed effect of the linear mixed model analysis for the effect of condition on asynchrony scores. **(A)** Asynchrony scores during pre stimulation (Pre), sham stimulation (S Stim) and sham post-stimulation (S Post). **(B)** Asynchrony scores during the three stimulation types: sham stimulation (S Stim), same-phase-same-frequency stimulation (S-F Stim) and different-phase-different-frequency stimulation (D-F Stim). Standard errors are indicated by horizontal lines.

**Figure 5** for a comparison of individual and dyad preferred tempo by condition. Linear regression analysis with the sum of both players' mean individual preferred tempo and the fastest mean individual preferred tempo as factors showed a predictive effect of the sum on variance in mean dyad preferred tempo [$F(40) = 10.77$, $p < 0.0005$, $R^2$ adjusted $= 0.317$; sum: $t(40) = 2.056$, $p < 0.05$)]. Linear mixed model analysis showed differential effects for conditions (combination of stimulation type and experimental segment) on dyad preferred tempo [$\chi^2(6) = 163.13$, $p < 0.0001$]. Relative to pre-stimulation, dyad preferred inter-tap interval was decreased in all other conditions (see **Figures 5**, **6**). Neither same-phase-same-frequency stimulation nor different-phase-different-frequency stimulation differed from sham stimulation [$t(2910) = 0.931$, $p = 0.352$; $t(3164) = -0.667$, $p = 0.505$]. The same was true for same-phase-same-frequency post-stimulation, different-phase-different-frequency post-stimulation and sham post-stimulation [$t(4610) = -0.415$, $p = 0.678$; $t(4714) = 0.107$].

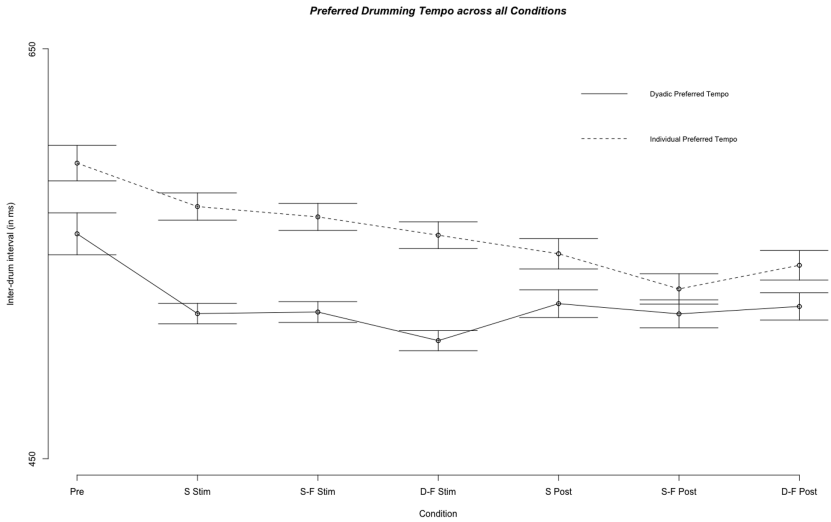


**FIGURE 5 |** Comparison of the fixed effect results of the linear mixed model analysis for the effect of condition on individual preferred and dyadic preferred drumming tempo for all experimental conditions. Displayed are mean inter-drum intervals as estimated by the model. Stimulation conditions: Pre, pre; S Stim, sham stimulation; S-F Stim, same-phase-same-frequency stimulation; D-F Stim, different-phase-different-frequency stimulation; S Post, sham post; S-F Post, same-phase-same-frequency post; D-F Post, different-phase-different-frequency post. Standard errors are indicated by horizontal lines.

# DISCUSSION

## General Discussion

The aim of the present study was to investigate how manipulation of ongoing inter-brain phase synchronization by hyper-tACS would affect the synchrony of dyadic drumming performance. Previous research showed that the real-time neural dynamics of various forms of interpersonally coordinated behavior are characterized by inter-brain phase synchronization (Konvalinka and Roepstorff, 2012). To our knowledge, and with the notable exception of Novembre et al. (2017, see below), previous studies that investigated inter-brain dynamics during interpersonal action coordination were observational in nature. The present study is an attempt to manipulate inter-brain dynamics and examine the effects of this manipulation on interpersonal action coordination.

The main result of the present study is that, compared to sham stimulation, only dyadic asynchrony was modulated by same-phase-same-frequency and different-phase-different-frequency hyper-tACS. Metronome asynchrony, individual preferred tempo and dyad preferred tempo were not modulated. Performance on all four behavioral measures changed between pre-stimulation and stimulation, and between stimulation and post-stimulation conditions under sham hyper-tACS: Dyadic asynchrony decreased while metronome asynchrony increased, and both individuals and dyads preferred faster tempi (see **Figures 2**, **5**). We suspect that the decrease in asynchrony for dyadic drumming from pre-stimulation to sham stimulation reflects learning or 'tuning-in' processes within a dyad. As subjects were very good at synchronizing to a metronome already in the pre-stimulation condition, the slight decrease in performance over the course of the experiment might reflect a ceiling effect. Under same-phase-same-frequency and different-phase-different-frequency tACS, metronome asynchrony as well as individual and dyad preferred tempo developed just as under sham stimulation, while dyadic asynchrony remained unchanged compared to pre-stimulation and increased compared to sham stimulation. This finding suggests that artificial modulation of naturally occurring inter-brain synchronization in the theta frequency range at frontocentral and centroparietal sites in the left hemisphere during joint action by hyper-tACS may actually impair, rather than improve, dyadic learning. Task difficulty as an alternative explanation for the differential effect of active tACS on dyadic asynchrony and metronome asynchrony is unlikely. Although participants notably synchronized better with a metronome than with each other during pre, this performance difference was no longer present during sham and post-sham. Here, dyadic and metronome synchronization performance were identical (see **Figure 4**). Thus, dyadic synchronization does not appear to be more difficult than metronome synchronization *per se*. Once subjects completed an initial practice period and presumably 'tuned-in' to each other, we observed no performance difference between metronome synchronization and dyadic synchronization.

Inter-brain synchronization appears to play a functional role in establishing interpersonally coordinated actions.

Contrary to our guiding hypothesis, we did not observe a differential effect of same-phase-same-frequency and different-phase-different-frequency hyper-tACS on dyadic drumming performance. It is possible that this results from person-to-person

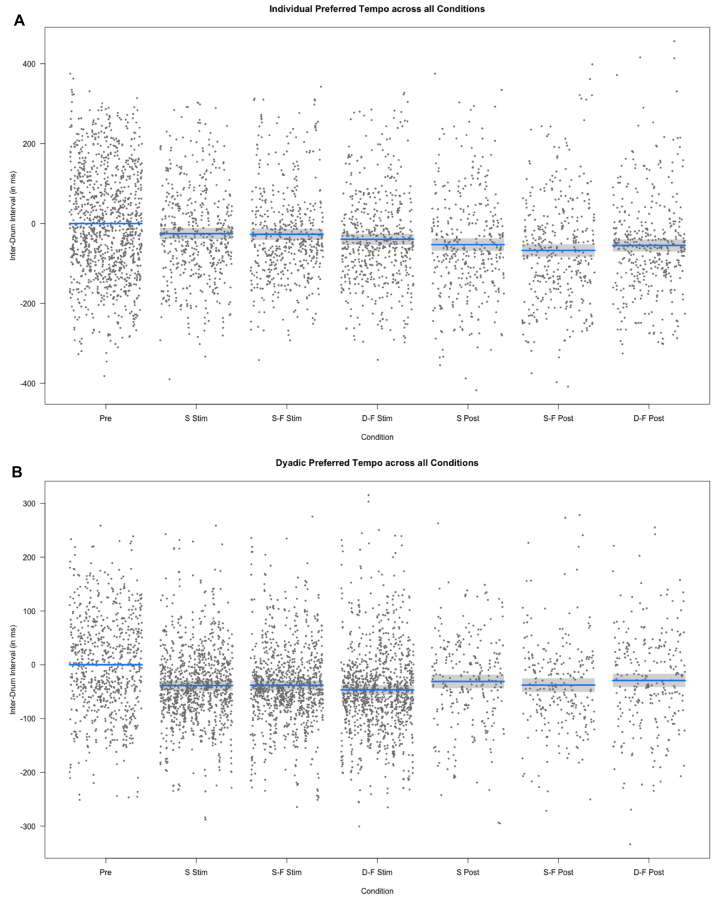


**FIGURE 6 |** Results of the fixed effect of the linear mixed model analysis for the effect of condition on individual and dyadic preferred drumming tempo. **(A)** Partial residuals as estimated by the mixed model for individual preferred drumming tempo. **(B)** Partial residuals as estimated by the mixed model for dyadic preferred drumming tempo. Stimulation conditions: Pre, pre; S Stim, sham stimulation; S-F Stim, same-phase-same-frequency stimulation; D-F Stim, different-phase-different-frequency stimulation; S Post, sham post; S-F Post, same-phase-same-frequency post; D-F Post, different-phase-different-frequency post. Blue lines indicate model prediction values. 95% confidence intervals are displayed as gray bands.

variation in the actual frequency of neural entrainment caused by tACS stimulation. It is known that tACS stimulation of a single location may produce a range of different effects at the neural level. For example, 10 Hz tACS applied over the motor cortex inhibits motor evoked potential but improves visuo-motor implicit learning (Antal and Paulus, 2013). More important, the efficacy of tACS depends on the power of endogenous oscillations in the individual's brain at the targeted frequency (Ruhnau et al., 2016) and the electrode placement protocol used in the present study left room for individual differences in electrical current flow (Datta et al., 2012; Cabral-Calderin et al., 2016). As a result of unique differences within each dyad, we might not have succeeded in boosting inter-brain synchronization precisely. Instead, individual differences in the neuronal response to our same-phase-same-frequency stimulation protocol might have resulted in neuronal entrainment at slightly different frequencies for the two members of the dyad. As a result, our same-phase-same-frequency protocol may in fact have resulted in an out-of-phase, out-of-frequency neuronal response.

We did not observe any performance increases when participants drummed in synchrony with a metronome whose frequency was harmonic to the tACS frequency. This null result might either be taken to support our operationalization to target coordination rather than pure motor processes, or to support the interpretation that hyper-tACS was not successful in boosting the same frequencies in both brains. While "there is need of online tACS/EEG evidence to open a new frontier in oscillatory brain rhythms investigations" (Feurra et al., 2012, p. 2) the separation

of tACS artifacts and brain activity in EEG (Helfrich et al., 2014) and MEG signals (Neuling et al., 2015) has only been pioneered recently and there is yet "no established method for precise source localization and artifact-free source reconstruction of tACS-entrained brain oscillations near and underneath the stimulator electrodes" (Witkowski et al., 2016, p. 89; see also Bergmann et al., 2016). Consequently, the present study does not directly assess the efficacy and precision of hyper-tACS in entraining inter-brain oscillations (see Limitations).

Further, correlations between behavioral performance and synchrony in inter-brain dynamics have only been reported in a few studies and often did not follow a linear 'more is better' principle. In a study using a turn-based card game paradigm, Babiloni et al. (2007b) reported that only participants belonging to the same team showed functional oscillatory connectivity. The authors also reported directed coherence between activity at frontal sides in the leader's brain with activity at frontal and parietal sides in the follower's brain (Astolfi et al., 2010). Such asymmetries in inter-brain dynamics within a dyad were observed in other paradigms too: Konvalinka et al. (2014) collected EEG hyperscanning data during a synchronized finger-tapping task. In contrast to tapping with a metronome, tapping with the other participant coincided with suppressed alpha and low-beta activity over central and frontal areas. In eight out of nine dyads, this suppression of alpha oscillations was more pronounced for the leader than for the follower during both task anticipation and execution. Jiang et al. (2015) assessed the relation between leadership and multibrain dynamics via functional near infrared spectroscopy (fNIRS) hyperscanning in a leaderless group discussion paradigm. The authors reported higher levels of inter-brain synchronization for leader-initiated communications compared to the ones initiated by followers. Sänger et al. (2012) also observed higher within-brain synchrony for the leader as compared to the follower while playing guitar in duet. Taken together, interpersonally coordinated joint action appears to be consistently characterized by changes in inter-brain coupling dynamics; however, in the case of lead-follow behavior these dynamics tend to be asymmetric and non-linear, comparable to dynamics of behavioral synchronization that show significant non-stationarity (Boker et al., 2011). Findings from two recent studies in our lab corroborate the importance of non-linear influences. These studies used graph theory measures to analyze the hyperbrain networks involved in joint guitar play (Sänger et al., 2013) and in romantic kissing (Müller and Lindenberger, 2014). This analysis technique makes it possible to capture more complex aspects of inter-brain dynamics. Sänger et al. (2013) detected different patterns of directed between-brain couplings for leader vs. followers, while Müller and Lindenberger included cross-frequency inter-brain dynamics into the analysis and could show positive as well as negative correlations between measures of inter-brain synchronization strength and kissing satisfaction. Taken together, the stimulation frequencies and topographies needed to facilitate sustained joint action coordination might be more complex and specific than broad right frontoparietal 6 Hz coupling. We included metronome asynchrony and individual dyad preferred tempo as control conditions for the study. As we did not observe any changes related to active tACS in any of the three measures, we conclude that the modulations observed in dyadic asynchrony are not due to a direct interference of tACS with individual motor processes but indeed result from interference of tACS with ongoing inter-brain dynamics. Novembre et al. (2017) recently showed that hyper-tACS applied over left centroparietal areas at 20 Hz improved the synchronization of the first four taps in a dyadic finger tapping task but not in later taps. Thus synchronization processes closer to the motor level appear to indeed have a prominent affect on inter-personal action coordination (initiation), although Novembre et al. (2017) used different stimulation frequencies within one session and thus possible confounds by tACS after-effects (Veniero et al., 2015) from stimulation blocks at 2 and 10 Hz cannot be excluded.

## Individual and Dyad Preferred Drumming Tempi

The range of individual preferred tempo found in the present study is comparable to the range reported in the literature (Fraisse, 1982; Kay et al., 1987; Moelants, 2002). Furthermore preferred tempi increased as a function of time which replicates findings by Collyer et al. (1994), who reported a tendency for individual preferred tempo to increase after a few trials. Distribution of dyad preferred tempo was comparable to the distribution observed with the same paradigm by Kleinspehn (2008).

To our knowledge, dyad preferred tempo, its relation to the tempi preferred by the two individuals within the dyad and its stability over time has not been systematically studied in a tapping or drumming paradigm yet. Interestingly, dyad preferred tempo was generally faster than preferred tempo in individual drumming. Like individual-preferred tempo, it increased after the pre-stimulation, potentially as a function of time (compare 9). Though faster, dyad-preferred tempi were characterized by lower inter-trial variance than individual-preferred tempi. The fact that preferred tempo increased when drumming dyadically may relate to the suggestion that interacting individuals decrease their temporal variability in an effort to make themselves more predictable and thus facilitate joint action (Vesper et al., 2011). The finding that the two individual-preferred tempi within a dyad explained variance in dyad preferred tempo, further corroborates this interpretation that an increase from individual to preferred tempo is not accidental, but mechanistic to dyadic drumming. Interestingly the sum of both individual preferred tempi explained more variance than the difference between individual preferred tempi or the faster/slower tempo alone. This might indicate that it is the interaction between the individuals and not the more dominant individual that gives rise to the speeding phenomenon in dyad preferred drumming tempo. Further research is needed that specifically investigates the mechanistic interplay between individual and dyad preferred tempi.

## Limitations

Due to methodological challenges in controlling current flow and precise neural entrainment with tACS, this present pioneering study lacks a validation to what degree the neural frequencies

of the interacting participants become more synchronized or desynchronized upon hyper-tACS. Thanks to recent advances in the field of non-invasive brain stimulation stimulation protocols that circumvent stimulation artifacts have been introduced, such as amplitude-modulated tACS (Witkowski et al., 2016), which allow for source reconstruction and mapping of entrained brain oscillations. Future studies combining hyper-tACS and EEG with refined stimulation protocols (Alam et al., 2016) are needed to overcome this limitation and to extend the findings of this present study. Consequently, the present study is limited in that it does not directly assess the efficacy and precision of hyper-tACS in entraining inter-brain oscillations. Future work using these techniques might be able to more precisely determine the actual induced frequency responses, and be able to account for differential individual responses to the tACS stimulation.

The stimulation protocol chosen further limits this study in that stimulation was delivered only to frontocentral and centroparietal areas in the right hemisphere at specific frequencies in the theta range. Future research is needed to verify if similar results could be obtained with different stimulation frequencies within the theta range. This setup might have prevented us from detecting effects of hyper-tACS on synchronization phenomena closer to the motor level. In a recent study Novembre et al. (2017) reported that hyper-tACS facilitated synchronized interpersonal action initiation, but not sustained action coordination, specifically when applied over centroparietal regions over the left hemisphere at 20 Hz with 0 degree relative phase different, but not when applied at 10 Hz, 2 Hz or with 180 degrees relative phase difference. Future hyper-tACS studies using more complex stimulation protocols targeting for example right centroparietal areas in the theta or mu frequency range (as a 'marker of social coordination') and centroparietal areas contralateral to the drumming hand in the beta frequency range (representing networks closer to the motor level) may extend our understanding of how inter-brain synchronization processes facilitate the initiation and sustention of inter-personal action coordination.

## CONCLUSION

The present study is an attempt to experimentally manipulate inter-brain dynamics and observe the effects of this manipulation on joint action performance. We operationalized this goal by applying same-phase-same-frequency and different-phase-different-frequency hyper-tACS during a dyadic drumming paradigm, where dyads were instructed to drum in synchrony with another participant. Contrary to expectations, we found a reduction in dyadic synchrony during active hyper-tACS when compared to sham tACS. This reduction was not evident when individuals were asked to synchronize to a metronome, nor paralleled by corresponding changes in dyadic drumming frequency or individual preferred tempo.

We suspect that the observed impairment in dyadic drumming synchrony in the same-phase-same-frequency tACS condition may reflect individual differences in the frequency entrainment induced by tACS. Further hyper-tACS studies with more precise stimulation protocols are needed that ensure oscillations in the same frequencies are entrained in the brains of two individuals engaging in joint action.

As a byproduct of the paradigm used, we observed specific relationships between individual and dyad preferred drumming tempi. The tempi preferred by the two individuals in a dyad predicted the dyad's preferred tempo. However, the dyad's preferred tempo was generally characterized by lower variance and higher frequencies than the tempi preferred by the individuals alone. The interplay between individual- and dyad-preferred drumming or tapping tempo might present a useful clues for a more mechanistic understanding of interpersonal action coordination.

## ETHICS STATEMENT

This study was carried out in accordance with the recommendations of Deutsche Gesellschaft für Psychologie with written informed consent from all subjects. All subjects gave written informed consent in accordance with the Declaration of Helsinki. The protocol was approved by the Deutsche Gesellschaft für Psychologie.

## AUTHOR CONTRIBUTIONS

CS, TB, VM, and UL designed the experiment. CS acquired the data. CS and TvO analyzed the data. CS, TB, VM, and UL interpreted the data. CS, TB, VM, and UL wrote the manuscript. CS, TB, VM, TvO, and UL approved the final version of the manuscript.

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## SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fnhum.2017.00539/full#supplementary-material

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**Conflict of Interest Statement:** The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.


**Neural Synchronization Patterns**
**During Interpersonal Action Coordination**

**Caroline Szymanski**

**2017**

**Eidesstattliche Erklärung:**

Hiermit erkläre ich, die Dissertation selbstständig und nur unter Verwendung der angegebenen Hilfen und Hilfsmittel angefertigt zu haben.